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THE NATURAL HISTORY OF THE SEA.

THE study of the sea and its inhabitants owes much of its extraordinary fascination to the fact that all our gains in knowledge are the outcome of methods of groping for the truth by the aid of instruments hid from sight for the most part, and resembling in their operation the ventures of the gambler. The voyager who, on a clear night, surveys the heavens and the deep sea beholds two regions of research in which natural knowledge is increased in very diverse ways. The marvellous certainty with which the astronomer can foretell the movements and even the existences of heavenly bodies, stands in sharp contrast with the element of chance which enters into the pursuits of the student of life in the deep sea. The naturalist is content to dip into this great lucky-bag with the pleased expectation that he will be rewarded. His methods of capture, primitive in their simplicity, or crude in their complication, are themselves in contrast with the perfected instruments and methods of examination brought to bear on the spoils of his victory over this intractable element.

The great sea-captains and explorers from the earliest times were geographers in search of fresh lands who used the sea as a means of transport, and all the tradition of mystery which grew up in their minds, and is still part of every seaman's nature, survives and tinges even the scientific work of examining the physical and biological conditions of the ocean. It is still the unexpected that happens to the

naturalist or the physicist who goes down to the sea in ships. This is owing to the fact that the study of the sea, and especially of the animals and plants in it, is yet in its youth, and the progress of our knowledge is not to be measured by the milestones of volumes recording the work and speculation of recent years.

The two magnificent volumes which close the record of the work of the *Challenger* Expedition (1) are in every way worthy of their fellows in the series of fifty containing the whole account of this celebrated voyage. It is just a quarter of a century since H.M.S. *Challenger* sailed on a voyage which was to make discoveries, comparable only with those of Columbus and his immediate successors. The ocean which covers three-fifths of our globe was barely known to us, though admirable research had been steadily increasing our knowledge and speculations for a century. As an introduction to the two volumes containing the "Summary of Results," Dr. John Murray has given an interesting historical account of oceanography from the earliest times, illustrated with a series of maps representing the growth of geographical ideas.

The ingenious arguments founded on neither experiment nor observation, which were indulged in up to last century as to the depth of the sea, etc., are typical of all other early ideas on the subject. Even while the mapping of trade routes was in an advanced state of development, knowledge of the ocean remained strictly superficial. Cook's First Voyage (2) in the *Endeavour* (1768-71), carrying Sir Joseph Banks and Dr. Solander as naturalists, marked the beginning of true observation of the sea. The *Journal* kept by Banks on this voyage, recently edited by Sir Joseph Hooker, has made known to us the fact that Banks was no mere gilded patron of science, but a genuine hardworking observer of nature who did not confine his work to the lands visited, but was incessantly occupied with the marine fauna and flora of the high seas.

The circumstances under which the *Journal* has at length been published after more than a century in one limbo or another, are extremely interesting. At one stage

of its history the original MS. came into the hands of Sir Joseph Hooker's grandfather, Dawson Turner, the celebrated phycologist, who had a copy made for him. While on a visit to his grandfather in 1833, Sir Joseph saw it being copied, and, in assisting to verify the transcript, naturally became fascinated with the story. After other adventures it reached the Manuscripts Department of the British Museum with some eventual condition of its becoming the property of the Trustees. Mr. Carruthers, then Keeper of the Department of Botany, succeeded in obtaining the Dawson Turner transcript for that Department, and in faithfully clinging to it. The original Banksian MS. and correspondence, however, were claimed from the Manuscripts Department in 1885 or 1886, on what appear to be slender grounds, by the late Lord Brabourne, who carried them off, and after some correspondence he declined the sum offered by the Museum for purchase of the Banksian MS., broke up the whole into lots and sold them at Sotheby's, the original MS. of the *Journal* going to an autograph dealer for £7 2s. 6d., whereupon it soon disappeared. This barely credible and discreditable story is told here, and no one can envy Lord Brabourne his reflections on receipt of this paltry sum for a document of national interest. The Dawson Turner copy in the Department of Botany has therefore been the means of saving the *Journal* from oblivion, and it has been used in Sir Joseph Hooker's edition. Besides giving us a fascinating account of Cook's momentous voyage, of such imperial importance to Britain, the *Journal* presents us with a picture of a naturalist's occupation on such an expedition, and of his work at sea. Banks' interest in marine life begins with his leaving Plymouth, and he faithfully records his observations, many of them at that time novel, as he proceeds. He gives, among other noteworthy entries, a good description of the banks of pelagic *Oscillatorieæ*, the "sea-sawdust," seen by him on the coast of Brazil, Torres Straits, and other places. "It was formed," he says, "by innumerable small atoms, each scarcely half a line in length, yet, when looked at under a microscope, consisting of thirty or

forty tubes, each hollow and divided throughout the whole length into many cells by small partitions, like the tubes of *Confervæ*. . . . A Portuguese, who came on board the ship at Rio de Janeiro, told me that at San Salvador, on the coast of Brazil, where the Portuguese have a whale fishery, he had often seen vast quantities of it taken out of the stomachs of whales or grampuses." When one remembers the minute size of the individual tubes and the kind of microscope Banks must have had, the description is marvellously accurate. This observation as to a Protophyte being found in quantity in the stomachs of whales is interesting in connection with the name of "whales' food" given to the masses of diatoms in the Arctic Seas. It was pointed out by the late Mr. R. Brown (Campst.) in 1868 (*Trans. Bot. Soc. Edin.*, vol. ix.) that the well-known discoloration of tracts of the Arctic Sea is owing to diatom life—principally the diatom now known as *Thalassiosira Nordenskioldii*. He found this and other diatoms in the intestinal canal of the small Entomostraca, Pteropodous Mollusca, Medusæ, etc. (the true whales' food), which frequent the discoloured tracts, and in turn live upon the diatoms. Thus it comes about that organisms, which individually are invisible without a high power of the microscope, ultimately furnish the food of the mightiest animals on our globe. In the Antarctic Seas the whales feed on minute animals closely allied to those of the Arctic, and these without doubt also subsist on the extensive tracts of diatoms of the southern ocean with which Sir Joseph Hooker himself, as it happens, first made us acquainted. The whales must inevitably swallow large quantities of the diatoms themselves in pursuit of the minute animals, as was probably the case with the whales mentioned by Banks, and it is possible that the mixed animal and vegetable diet may be beneficial. This observation of Banks is cited merely as showing the living interest his *Journal* possesses to students of the sea at the present day. There are few pages of it that do not show him to be, as Sir Joseph Hooker truly says, "the pioneer of those naturalist voyagers of later years, of whom Darwin is the great example".

Cook, on the conclusion of his voyages, left little to be done in the way of discovering new lands, and gradually attention came to be given more particularly to the scientific study of the sea. Just as Banks was the first notable observer of animal and plant life on the high seas, so the physical study of the sea may be said to spring from Cavendish's self-registering thermometer, first made about 1757. He suggested that it might be applied to ascertaining "the temper of the sea at great depths". Irvine, who accompanied Lord Mulgrave to the Arctic regions, so applied it in 1773 (two year after the return of the *Endeavour*), and he also seems to have invented a water-bottle. On this voyage, also, one of the earliest attempts at deep-sea sounding was made, the greatest depth reached being 683 fathoms. Improvements in apparatus were made, and many experiments were tried in the succeeding years. Franklin, Sir John Ross, and among naturalists the great Ehrenberg were conspicuous by their labours. Sir James Clark Ross's Antarctic Expedition (1839-43), and at the same time Captain Wilkes, who commanded the first purely scientific expedition sent out by the United States, made notable advances. The one expedition was fortunate in carrying Sir Joseph (then Dr.) Hooker, the other Dana, as naturalist. However, after all was done, there was still lacking the material for any important generalisation. Edward Forbes, Captain Spratt, Maury, and many others continued to amass observations and to attract attention to the study by theoretical views of profound interest. Captain Dayman, who sounded across the North Atlantic in H.M.S. *Cyclops* (1857), brought home soundings in which Huxley discovered the Coccoliths. It was not, however, until submarine telegraphy came to be a necessity that any great opportunities came for a systematic study of the deep sea, just as ocean commerce has led to the careful charting of coasts and shallow seas. In 1860 H.M.S. *Bulldog* made a survey for a telegraph route between England and America. It was on this voyage that Dr. G. C. Wallich made his celebrated observations on the existence of a special deep-sea fauna. Many of his opinions have been confirmed by

subsequent researches, and they exhibit an industry and insight of a wholly remarkable character. His discoveries were followed up by Torell, Pourtalès, Agassiz, Wyville Thomson, Carpenter, Gwyn Jeffreys and others, until the *Challenger* Expedition became a necessity. This expedition and the publication of the fifty magnificent volumes of results are a monument of what the British Government has done, and can do, for science. It is being so constantly dinned into the ears of the tax-paying public that our Government does nothing for science, but leaves its advancement almost solely to private enterprise and the Universities, that national pride is apt to fall to zero in the matter. National scientific institutions like the Royal Navy, the British Museum, Greenwich Observatory, Kew Gardens, are always with us in their pretended poverty, and it is significant of our national habit of grumbling that Dr. John Murray in his preface to this concluding volume of the *Challenger* Reports feels it a sacred duty to say that: "The majority of the authors of the special memoirs have spent years in the examination of the collections and in the preparation of their manuscript and illustrations for the press, without other remuneration than either a copy of the *Challenger* publications or a small honorarium to cover the outlay necessitated by their researches. The payments to the Civilian Staff have been very moderate, and in my own case, at least, have not covered actual expenditure in connection with the work of the Expedition." He tells us that, in 1889, the Treasury declined to ask Parliament to renew the annual grant, and after correspondence in which Dr. Murray offered "to finish the Report at my own expense," the Government granted £1,600 for the completion of the volumes, and somehow they have been completed. Dr. Murray has happily survived these privations, and appears in all respects as if they had done him good. Moreover, it would have been a pity if the Treasury had not been true to itself in the course of this great undertaking.

These final volumes contain besides the historical sketch (the substance of which ought to be republished

as a hand-book, together with a brief account of the results of the *Challenger* Expedition) a detailed summary of results obtained at all the observing stations, making a scientific log of the voyage as well as an index to the special memoirs. The summary occupies the main part of the two volumes, and is illustrated with a series of valuable maps and sections. Following the summary is an analysis of the bathymetrical and geographical distribution, itself a gigantic labour, an index of the genera and species, and a general index. These are labours the outcome of which will appear only when years of reference to them will have proved their value. The present interest lies in the much too brief general observations Dr. Murray permits himself to make. One result that was perhaps little expected is that only a relatively small percentage of deep-sea animals have a wide distribution over the floor of the ocean. Alexander Agassiz, as the result of work with closing tow-nets in the *Albatross* so recently as 1891, concludes that "in the open sea, even when close to the land, the surface pelagic fauna does not descend beyond a depth of 200 fathoms, and that there is no intermediate pelagic fauna living between that depth and the bottom, and that even the free swimming bottom species do not rise to any great distance, as we found no trace of anything within sixty fathoms from the bottom, where it had been fairly populated". He thinks, however, that "in a comparatively closed sea, at a small distance from the land, there may be a mixture of the surface species with the deep sea bottom species". Dr. John Murray, however, states that: "The tow-net experiments carried out on board the *Challenger* during several years in all parts of the world led me to the conviction that these intermediate regions were inhabited, although with a much less abundant fauna than the waters near the bottom or those near the surface of the ocean". It is plain that there is here a field for future experiment and observation, especially when a trustworthy closing tow-net shall have been invented,—a simple one that may be used without waste of time and temper. Dr. Murray proceeds to contend that the organisms obtained

by the *Challenger* Expedition from the intermediate depths appear to have a much wider horizontal distribution than the surface fauna, and that they obtain their food by the capture of the dead organisms continually falling from surface to bottom. Agassiz will certainly have some difficulty in meeting his final argument. "It is well known that the deposits at the bottom are in most regions chiefly made up of the dead shells and skeletons of surface organisms. We have no definite ideas as to the rate at which these surface creatures may be falling to the bottom, but it is evident that nets which have been dragged in these intermediate depths on the opening and closing principle, without capturing any of these falling organisms, have either not been dragged for a sufficiently long time and through a sufficiently great extent of water, or have not worked successfully." Those who have not themselves invented opening and closing tow-nets, but who have yet worked with them, will recognise the force of the last four words.

The exploration of the sea has proved to be of exciting interests to geologists. The mere mention of the subject of the "permanence of continents" causes angry passions to rise. It is more than probable that there are yet "crowns to be broke" over this momentous discussion. L. Agassiz thought, so long ago as 1869, that the present continental areas within the 200 fathom line, as well as the oceans, have preserved their outlines and positions from the earliest times; that they have "remained essentially the same through all geological ages, varying only as to their relative height and depth as well as to their respective extension". Passing over the passionate utterances of geologists, which may have all the value claimed for them, we get now the testimony of this other great explorer of the deep sea. Dr. John Murray contends that: "It is most probable that the Ocean Basins were not so deep in these early ages, and numerous islands probably existed in them, with rocks similar to those that now make up the bulk of continental land. Possibly these former land-masses now form the submerged bases of the groups of oceanic islands wholly consisting, so far as we can see, of erupted rocks. In the

gradual evolution of the surface features of the planet, continental land appears, on the whole, to have become more compact, more circumscribed and higher, while the Ocean Basins have become more shut off from each other and deeper. Continental land has been far from permanent, but there are many reasons for believing that the areas on the surface of the planet, within which the present continents are situated, are areas within which continents have been torn down and built up again since the dawn of geological history, while similar revolutions have not taken place in abysmal or pelagic areas of the Ocean Basins to anything like the same extent, and not at all during any of the later geological periods."

Many naturalists besides the authors of the *Challenger* Memoirs have called attention to the striking resemblances between the Arctic and the Antarctic faunas and floras—both littoral and pelagic. So long as there has been climate on the globe, and geologists can point to no trace of it before Mesozoic times, these areas have been separated by the heat barrier of the equatorial zone. It is only fair to suppose that they are derived from a common stock. In an examination of this problem together with the origin of the deep sea fauna, and in seeking an explanation of the fact that the Arctic Ocean was probably a warm coral sea in palæozoic and even later geological times, Dr. Murray brings forward a daring hypothesis, which will no doubt meet with both criticism and ridicule. It has the merit of simplicity, the further one that nobody can deny it, and its spirited author may well ask astronomers and others for a better one. "The waters of these ancient oceans must have had a temperature of 65° or 70° Fahrenheit at the poles," and, "the same temperature and the same marine fauna prevailed from equator to poles, the temperature not being higher at the equator. . . . In early Mesozoic times cooling at the poles and differentiation into zones of climate appear to have commenced, and temperature conditions did not afterwards admit of coral reefs in the polar area. But the colder and hence denser water that in consequence descended to the greater depths of the ocean carried with it a large

supply of oxygen, and life in the deep sea became possible for the first time. There have been many speculations as to how a nearly uniform temperature could have been brought about in sea-water over the whole surface of the earth in early geological ages, as well as to how sufficient light could have been present at the poles to permit of the luxuriant vegetation that once flourished in these regions. The explanation that appears to me the most satisfactory is the one which attributes these conditions to the very much greater size of the sun in the early stages of the earth's history—an idea first introduced into geological speculations by Blandet, who likewise discussed the relations of Arctic and Antarctic faunas—together with the greater amount of aqueous vapour in the atmosphere, and the greater mass of the atmosphere." The pelagic Algæ, Radiolaria and Foraminifera, he holds, are probably the but slightly modified descendants of a very ancient universal pelagic fauna and flora, and life in its simplest form most likely first appeared in Pre-Cambrian times in the detrital matters laid down about the mud-line, when the mud-line was not so deep, and the land surfaces were more extensive than at the present time. These speculations are not stated without a gallant array of facts, and if the style of their exposition be somewhat insistent it is inspired by the fire of enthusiasm. The theory is comforting to the naturalist. Criticism must come from the student of solar physics and from the geologist. It may quite possibly prove that the Arctic fossil coral reefs are mostly, if not all of them, Bryozoa reefs—the point needs further research—and it may be that botanists have accepted on evidence that is not quite so convincing as was formerly supposed Heer's contention that Greenland once had a warm climate,—in short the provocation for Dr. Murray's theory may be less slender, but it is hard in any case to get over the evidence of massive calcium carbonate organic deposits in ancient Arctic seas always associated with warm waters, or the occurrence of veritable fossil tree-ferns like *Dicksonia* in Greenland.

Appended to the second part are two belated special memoirs, that on *Spirula* by the late Mr. Huxley and Dr.

Pelseneer, illustrated by Mr. Huxley's beautiful drawings, and the *Report on Oceanic Circulation*, by Dr. Buchan, with sixteen valuable maps.

Since the return of the *Challenger*, marine exploration has been carried on by the United States ships, *Tuscarora*, *Blake*, *Albatross*, *Gettysburg* and *Enterprise*, the German *Gazelle*, and the *National* or Plankton Expedition under Hensen in the Atlantic, the Norwegian *Vöringen*, the Prince of Monaco's *Princesse Alice*, the Italian *Washington* and *Vettor Pisani*, our own *Knight Errant*, *Triton*, etc., and by the Swedish Government in the Baltic and North Sea. Last of all much is to be expected from the work of the *Fram*. All the ships cited, and many others, have been steadily gathering facts; but to the naturalist perhaps none of them, since the *Challenger*, has gained such a harvest of interesting results, worthily published, as Hensen's Plankton Expedition. It would be out of the question to attempt more than notice of some of the weightiest results recorded in the publications of the voyage. Among those of general interest the researches of Bernhard Fischer (3) and Franz Schütt (4) claim particular attention.

Among the dark places in our knowledge of the economy of the sea there have been until recently two in particular urgently calling for more light. It has been a commonplace reflection of sea naturalists for many years (though Dr. Fisher appears to think it an original idea of Hensen's) that the minute free floating plant life of the sea must furnish the pastures of the animal life of the sea. The crucial observations, to be noticed presently made by Professor McIntosh and Mr. George Murray (7) settle by proof the actual fact of the diatoms affording sustenance to the animals of the sea—a fact long foreseen, but not until recently established in a satisfactory manner. The other crucial point has been determined mostly by Dr. Fischer himself. His early observations on a voyage to the West Indies in S.M.S. *Moltke* (1885-86) and his subsequent work during the Plankton Expedition, taken together with the researches of Russell and others, testify abundantly to the existence of

bacteria in the ocean where they play (as on land) the part of middleman between death and life, by causing the putrefaction of dead bodies of animals and plants—in other words by transforming dead organic substance into simple inorganic combinations to be used by plants and thus restored to the circulation of organic matter. This circulation of organic matter, as we know it on land, has hitherto been only guessed at in the deep, and Dr. Fisher and Messrs. McIntosh and G. Murray have, as it were, completed the two gaps in our knowledge of the circle.

Very little was known of the existence of bacteria in the sea when the Plankton Expedition sailed. Dr. Fischer had made his earlier observations, and after the return of the expedition, and before the publication of his memoir, Dr. Russell[1] made investigations in the Bay of Naples; these with the work of De Giaxa[2] practically exhaust the literature of marine bacteria. That the bacterial contents of the sea are being constantly influenced by the land is a fact beyond doubt. The sea is not only constantly receiving bacteria from the land, but all manner of such substances as nourish bacteria. A very poor estimate can be formed of the numbers carried by the winds to the sea, but we know that the rivers which are, many of them, little better than drains of organic matter are every moment conveying myriads to the sea. Nothing is more astonishing, however, than the rapid manner in which the sea, as it were, disposes of them. De Giaxa and Russell made experiments at varying distances from the opening of the sewer canal at Naples, and they found that at three kilometres from the shore the influence of the land was no longer recognisable. Similar observations made at Kiel, where the haven is more land-locked, gave a slightly different result, but it may be taken as generally true that the coastal waters, often very rich in bacteria near the shore, are generally quite free from the influence of the land in this respect at from three to five kilometres out to sea. Even, however, at places farthest removed from land, bacteria are present as a rule and at

[1] *Zeitschrift für Hygiene und Infectionskrankheiten*, Bd. vi. [2] *Ibid.*

considerable depths. In 1891 Russell found them on the floor of the Mediterranean itself fifteen kilometres from land at a depth of 500-600 fathoms. Their vertical distribution in the ocean may be summed up as scarce in the surface layers, increasing downward to 100 fathoms, occurring regularly to 200 fathoms, but steadily diminishing from 100 to the depths between 400-600, beyond which they have not been traced with certainty. It appears, moreover, fairly certain that the destructive action of sunlight is the cause of their scarcity at the surface, that they increase with the darkness, and reaching an optimum of general conditions of life at 100 fathoms, decrease again with the lowering of the temperature and the increase of pressure. Bacteria at 500-600 fathoms must undergo a pressure of over 100 atmospheres, and though it is known from experiment that they survive considerable pressures yet the vast pressures of the deep sea may be expected to reckon as a factor in determining their range in depth. Temperature also must play an even more important part. In the Mediterranean, where Russell's observations were made, the bottom temperature is constantly 13° C. all the year round, below about 100 fathoms, while above that it varies with the seasons. In the ocean the bottom temperature at great depths is always so low that no development of bacteria could be expected. The bottom of the Atlantic is either extraordinarily poor in bacteria or wholly free from them, the observations not being conclusive. In fact below 400 to 600 fathoms there is no certain record. These are the depths to which one would assign in fact the graveyard of the dead sinking surface plankton. That sunlight is, as every known fact would indicate, the cause of the scarcity in the surface layers is proved further by the fact that the strong light of summer periodically reduces the quantity in the upper waters.

Marine bacteria are moreover of peculiar sorts, though morphologically they resemble their land allies in adopting the well-known globular, rod-like and spiral forms. The luminous forms are confined to the coastal waters for the most part where they are found regularly on fishes, etc.,

and are in fact more abundant on them than in the surrounding waters. The forms peculiar to the high seas are of a very few species, but these have a wide distribution. From the fact of this general distribution and their development on dead animals and plants, Fischer makes the safe inference that they play the great and necessary part of putrefactive organisms in the economy of the sea, keeping the waters from becoming choked with dead organic matter, breaking this up and restoring it to circulation. There is as yet no evidence that the sea bacteria are able to cause diseases in the bodies of marine animals. Inoculation experiments by which the luminous forms caused the death of mice (the bodies of which subsequently exhibited phosphorescence) may be significant or may be misleading just as one is sanguine or cautious. The whole investigation of marine bacteria is yet in its infancy, and comparatively local in its results, but its advancement will undoubtedly throw an interesting light on the general study of these organisms.

Dr. Schütt, who with Dr. Fischer was one of the naturalists of the German Plankton Expedition, has made a minute and careful study of the little-known group of *Peridiniæ* (4 and 5), which form, together with the diatoms, the great bulk of free-floating marine vegetation, especially in temperate regions and near coasts. They are familiar to all from being the source of the luminosity or phosphorescence of our seas in summer and autumn. While diatoms are most abundant in our seas in the spring months, there are very few *Peridiniæ*. In summer and autumn the diatoms, though still plentiful, give place to enormous quantities of *Peridiniæ* which continue fairly abundant until about December, when they wane before the gradual predominance of diatoms again. They are a remarkable group, and our knowledge of their structure is due more to zoologists than to botanists from the rooted disinclination of the latter to use tow-net and microscopes at sea. The shore-loving botanist, however, will have to find his sea-legs before long, since so many problems are being submitted to him by the few who have ventured on the ocean

in search of work. From the researches of Dr. Schütt and several distinguished predecessors, it appears that we must regard the *Peridinieæ* (and some allied minor groups) as related to the diatoms from the structure of their membranes, mode of division, chromatophores, etc. Their membranes are not silicified like those of the diatoms, their valves frequently consist of several plates, their girdles are of different structure, they possess propelling whip-lashes, but in all or most of the points of difference the parts in question are comparable each with each, though the homologies, as Dr. Schütt states them, may appear sometimes a little strained. The new shells or valves of the *Peridinieæ* not being produced within, or overlapped by, the older membranes, they do not steadily diminish like the diatoms, and their life history is therefore not complicated by the production of auxospores. Moreover they appear to play the same part in the economy of the sea, as the diatoms do, in furnishing with them the great bulk of the nutriment for marine animals, the basis of most fishery problems. Dr. Schütt in the latter of the two works cited deals with some of the allied minor groups, such as *Gymnodiniaceæ*, the inclusion of which may be questioned by some authorities. As for *Pyrocystis* (the source of tropical luminosity in many cases) be it a state of *Noctiluca* as Moseley, Bütschli and others have contended, or be it a plant as others still hold, its place is at all events not in *Gymnodiniaceæ*. This part is in several respects the least satisfactory of Dr. Schütt's work, and his treatment of the diatoms (Bacillariaceæ) will meet with adverse criticisms from the special students of these organisms. However all owe him thanks for the compendious account of the whole series given in *Engler und Prantl* (5).

Diatoms have so long been a weariness to every naturalist, other than the sect of devotees of their study, from the fact that this study has consisted of mere records of markings and the performances of particular high power lenses mixed with unscrupulous jugglings in the nomenclature of forms, that it is refreshing to come upon discoveries of living interest to cultivated readers of natural

history. Mr. Comber (6) has placed some early observations by Lauder and others together with his own acute investigations, with the result that there is now a firmly established knowledge of the production within diatoms of other forms with different sculpturing of the tiny shells, probably in fact a dimorphism which may or may not occur in alternate order. Mr. George Murray (7), working at sea on the *Garland* on behalf of the Fishery Board for Scotland, independently established the same point by observation of the living forms and carried the matter further. He points out that the internally produced form (dealing with different genera from those of Mr. Comber) may itself multiply indefinitely in the sea before recurring to the parent form, and that not one merely but groups of two, four, eight, or sixteen of such forms may be produced within the parent, and that these are in certain cases not different from the parent but exactly resemble it. These details, important and utterly unexpected though they be, absorb the interest of the botanist more than that of the general student. Just as the great work of Russell, Fischer and others on the Bacteria of the sea has furnished us with a missing link in the chain of economic relationships of organisms, so another such link has been found, or rather strengthened, in Mr. George Murray's observations. Reference has been made to the observations of Mr. R. Brown on the occurrence of diatoms within the intestinal canals of the animals which form the food of whales, and their presence within many sea animals from full-grown fishes downwards is a well-known fact. That the plankton or surface floating plant-organisms are the basis of animal nutrition in the sea has long been obvious, but direct observation has been wanting. Mr. Murray made a minute examination of the substances digested by the Copepoda and other small crustacea, which themselves form a large part of the food of fishes, with the result that he has discovered such substances to consist almost exclusively of the chromatophores or colouring granules and fine fragments of the siliceous shells of diatoms. Professor McIntosh anticipated this observation, having made a brief record of the

fact without details in an account of other matters in a previous Fishery Board Report. Search was made by Mr. Murray for evidence of these animals eating *Peridinieæ*, but without success, possibly owing to the more easily destructible character of these organisms within the digestive tract, probably to their escape in many cases from being devoured by reason of their frequently spiny character. This seems to be the more likely since he failed to discover traces of spiny diatoms being eaten, and the beautiful sculpturing of diatom shells may come to be reckoned with the thorns and prickles of land plants as defences against animals! That young fishes themselves eat diatoms appears to be the case. He took young sand eels, young flat fishes and young clupeoid fishes, and reduced them to a fine ash which was found to contain considerable quantities of different diatoms, not broken as they would have been had they been eaten previously by small crustacea. Whitebait would appear from these experiments to be worthily fed on the beautiful diatom *Coscinodiscus*. As "all flesh is grass" in the strictly physiological sense, so all fish appears to be diatom. These organisms hitherto known to us as yielding the material for dynamite, polishing powders, and the amusement of harmless old gentlemen with microscopes, must in future be treated with becoming respect.

It undoubtedly represents an advance in methods of work when a fast mail steamer can be converted into a plankton expedition by simply taking a passage on board of her and pumping sea water from the deck hose through a fine silk bag and retaining the filtered substance for examination. Messrs. Murray and Blackman (9) have done it even more economically by capturing Captain Milner of R.M.S. *Para*, providing him with the apparatus and a little instruction, and sending him forth to look in the Atlantic for objects requiring an immersion lens to disclose their appearance.

By this means they obtained for study not only the Coccospheres and both kinds of Rhabdospheres, but *Pyrocystis* as well—a remarkable haul of debateable organisms. Their examination of them, briefly recounted, tends to confirm the view taken of them in the "*Challenger*" *Narrative*,

but evidence of their actual plant characters is yet incomplete and must remain so until competent observers have studied them alive. However, after the doubts thrown on the very existence of the Coccospheres and Rhabdospheres by the Hensen Expedition it is refreshing to find our countrymen vindicated. Captain Milner certainly deserves congratulation on having accomplished in a mail steamer, keeping contract time, what a thoroughly equipped German National Expedition failed to effect.

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GEORGE MURRAY.

THE VENOMS OF THE TOAD AND SALAMANDER.

BOTH in ancient and modern times a belief in the venomous nature of the toad and of the salamander has been almost universal, and many passages referring to this are to be met with in the writings of Aristotle (B.C. 332) Theophrastus (B.C. 322) Pliny and Dioscorides (A.D. 79). Shakespeare also alludes to it in several places, for example, a toad which had "sweltered venom sleeping got" was the first, and hence presumably the most important of the ingredients in the Witches' Cauldron in "Macbeth". Pliny is especially emphatic with regard to the salamander —"of all venomous beasts there is none so hurtful and dangerous as the salamander," and he goes on to say that the venom is narcotic and resembles aconite in its action. Until quite recently, if not at the present time, there was a popular idea in the West of England that a dog which worried a toad became mad.

The toad formerly had a place in the materia medica—in Spielman's *Institutiones Materiæ Medicæ* (A.D. 1784) two preparations are mentioned, "bufones exsiccati," dried toads, and "cineres bufonum," ashes of toads, the former being described as useful in bleeding from the nose and the latter in dropsy. The employment of preparations of the toad as remedies for dropsy is not so absurd as may at first appear, for it will be seen later that a substance is secreted by the skin very like digitalin, and hence possibly having a favourable effect in cases of cardiac dropsy.

Fact is often as strange as if not stranger than fiction, and the result of a number of investigations will be found to confirm the traditions mentioned above, much as they have been derided. If a toad (*Bufo vulgaris*) or a salamander (*Salamandra maculosa*) be examined, it will be found that the dorsal region and limbs are studded with numerous warty prominences, and in the toad there is also a large elongated gland on either side of the neck which has been

termed the parotid gland. These are the "venom glands" and their secretion, the "venom," is a white milky fluid, intensely bitter and somewhat acrid to the taste, which exudes on pressure, on electrical stimulation, or after death by chloroform narcosis; in the latter case every gland will be found to be tipped by a white milky bead of the secretion.

Several observers (1) have studied the histological characters of these glands, which, as they have essentially the same structure in each animal, may be described together. The gland follicles are more or less globular and communicate with the surface by a short duct. The lining membrane of the larger follicles is thrown into folds forming imperfect septa which project into its cavity and are covered with a flattened epithelium. In the smaller follicles these septa are wanting, and the lining epithelium is more or less cubical. The walls of the follicles are plentifully supplied with nerves and blood-vessels.

That these cutaneous glands in both the toad and salamander really do secrete a venom which is extremely toxic when introduced into the circulation is acknowledged by, and is moreover conclusively proved by the experiments of, all investigators with the exception of Davy (2 and 3) and Rainey (1) who failed to observe any ill effect from the secretion of the toad, their failure being due perhaps either to the administration of too small a quantity of the venom, or because of its non-absorption into the circulation, probably the latter. The production of venom is by no means confined to the common toad and land salamander, but is met with in allied species,—the natterjack and tropical toads, the tritons, and to a small extent the frogs. The creatures are unable voluntarily to eject the venom, which is secreted only in response to some reflex irritation and has a purely defensive function.

Pelletier (4) in 1817 appears to have been the first to investigate chemically the venom of the toad. He found that it was acid in reaction and partially soluble in alcohol. A fuller examination was made by Davy (2) in 1826 who describes it as a yellowish thick fluid the greater part of

which is soluble in water and in alcohol, its solution not precipitated by lead acetate and only slightly by corrosive sublimate, and giving a purple colour with nitric acid; the alcoholic extract being "very acrid, acting on the tongue like extract of aconite".

Gratiolet and Cloez (5) in 1852 by treating the dried venom with ether, evaporating the ethereal solution and extracting the residue with alcohol, separated the active principle more or less completely and found that it was entirely soluble in water acidified with hydrochloric acid, this solution being precipitated by bichloride of platinum and by corrosive sublimate. They considered that these and other facts seemed to establish the probability of the existence of an alkaloidal substance in the venom. Twenty years later their surmise was proved to be correct by Casali and Fornara (6) who succeeded in extracting by the Stas-Otto process an alkaloid to which they gave the name of phrynine or bufidine and possessed of the following properties—a white amorphous solid, slightly soluble in water and very soluble in alcohol, ether and chloroform. It gave precipitates with picric acid, platinic chloride, and iodic acid, but not with lead acetate (*cf.* Davy) nor with potassium ferrocyanide and acetic acid. They were unable to ascertain its percentage composition, as the amount of material at their disposal was limited. Calmels states that the venom of the toad contains methylcarbylamine and isocyanacetic acid (7).

The writer has recently examined chemically the cutaneous secretion of the toad. It is a thick milky fluid, acid in reaction, drying quickly in the air, forming a yellowish amorphous solid almost completely soluble in alcohol but only partially so in water, the solution being very bitter. The secretion and glands from several toads were placed in absolute alcohol where they remained for some time, the alcoholic solution was then filtered off and evaporated, and yielded a greyish amorphous residue which was slightly soluble in distilled water and more so in water acidified with hydrochloric acid. The solution gave precipitates with iodine in potassium iodide, gold trichloride, platinum bichloride, Nessler, and picric acid, the latter one dissolving

completely on heating and reappearing on cooling, it gave no precipitates with mercuric chloride, cupric sulphate, ferric chloride, and potassium ferrocyanide and acetic acid. These reactions indicate the presence of an alkaloid and the absence of any proteid body. The solid residue gave an orange-brown colour with sulphuric acid, an inky-brown colour with nitric acid, a reddish colour with sulphuric and nitric acids, a brown becoming purplish with sulphuric acid and a trace of bromine, and a greenish colour with hydrochloric acid on warming. These reactions are not unlike those yielded by digitalin.

The first observation on the chemical nature of the venom of the salamander seems to have been made by Gratiolet and Cloez in 1851 (8). They describe the venom as being a whitish milky fluid possessing a strong penetrating and disagreeable odour, acid in reaction, coagulating quickly on exposure to the air and instantly on the addition of alcohol: in this it differs from the venom of the toad. A little later Vulpian gave a similar account of it (9). Zalesky in 1866 (10) made a very complete examination of this venom and succeeded in extracting an alkaloidal body. The venom was diluted with water, heated, filtered to separate a coagulum, and the filtrate precipitated by phosphomolybdic acid. The precipitate was dissolved in baryta water, the barium precipitated by a current of carbon dioxide gas and filtered off, and the filtrate concentrated over a water-bath in a current of hydrogen. Long needle-shaped crystals were obtained which on complete drying formed an amorphous mass soluble in water and giving an alkaline solution which was precipitated by phosphomolybdic acid and by platinic chloride. The composition of this alkaloid is expressed by the formula $C_{34}\,H_{60}\,N_2\,O_5$ and its hydrochlorate by $C_{34}\,H_{60}\,N_2\,O_5,\,2HCl$. Zalesky named it Samandarine (from the Persian Samandar, whence Salamander), but subsequent writers have invariably termed it Salamandrine. It will be evident from the foregoing that the active principles of the venoms under consideration are totally different substances from those of snake venom, the former being alkaloidal while

the latter are proteid in nature (11). Both venoms have a special action on the nerve centres. Gratiolet and Cloez (8) found that 2 milligrams of the dried venom of the toad when injected subcutaneously killed a greenfinch in fifteen minutes with convulsions and loss of co-ordination. Vulpian (12) and later Couty (13) observed that this venom when placed in a subcutaneous wound was fatal to dogs and guinea-pigs, but when administered by the mouth produced nothing more serious than vomiting, the fatal event in the former case being preceded by excitement and vomiting and sometimes by convulsions. Placed in contact with the skin of frogs and tritons it is absorbed and kills them in from two to three hours (14).

Fornara (15) has shown that phrynin has an action on the respiration and circulation very like digitalis, it induces contraction of the arterioles and rise of blood pressure, increased cardiac contraction and diuresis. According to Phisalix and Bertrand (16) the blood of the toad is toxic from the presence of some of the active principle phrynin; 2 c.c. injected into a frog begins to produce symptoms within five minutes, and in fifteen minutes the pupils are contracted and hind legs paralysed, while 5 c.c. quickly kills a guinea-pig.

The venom of the salamander differs from that of the toad physiologically by its predominant convulsive action and by its inactivity on the heart. In the experiments of Gratiolet and Cloez (8) small birds such as chaffinches inoculated with it suffered from epileptiform convulsions, and paralysis followed by death in from six to twenty-six minutes; but mice and guinea-pigs though severely affected ultimately recovered. Vulpian (9) found that the venom was fatal to dogs in from two to three hours, to guinea-pigs in nine hours, and to frogs and toads in five hours. Its action on frogs was studied by Roth (17): convulsive movements are first induced, followed by paresis and paralysis of all voluntary movements. The heart's action remains normal for several hours after the cessation of all voluntary and reflex action.

Zalesky (10) observed that salamandrine produced

tremor, epileptiform convulsions, opisthotonos and death, and later experimenters have generally used this alkaloid or its hydrochlorate. According to Phisalix (18) the minimal fatal dose of the latter administered by subcutaneous injection is for the mouse $\frac{1}{10}$ of a milligram and for the dog about 1·8 milligrams per kilogram of the body weight. Intravenously the poison acts rapidly and in smaller doses. By the mouth the dose has to be much larger, for example, administered in this way, 10 milligrams on the mouse and 20 milligrams on the guinea-pig has little effect, and on the dog to produce appreciable symptoms the dose has to be increased to 8 milligrams per kilogram of the body weight. An interesting point is that when given by the mouth the fresh venom is more active than the hydrochlorate of the alkaloid.

Phisalix and Langlois (19) exhaustively studied the physiological action of salamandrine. The earliest symptoms of poisoning in the dog are restlessness, salivation, vomiting and tremor. Convulsions soon follow during which the temperature rises rapidly, the respiration being affected solely as a part of the general muscular spasm during their occurrence. It has no direct action on the heart though the vaso-motor system may be implicated to a slight extent. The post-mortem appearances are congestion of the principal viscera, hæmorrhagic points in the diaphragm and heart muscle, and emphysema and hæmorrhages in the lungs. The meninges are congested and the pia mater of the fourth ventricle is studded with hæmorrhagic points.

Many other interesting features in the action of the venom have been observed by Dutartre (20). Salamandrine, unlike the active principle of the toad's venom, is not found in the blood nor is it present in the tadpole. The venom has little or no action on the snail and slug, in crickets it produces convulsions followed by a lethargic state which passes off in about twenty-four hours and the insects recover, while not only are bacteria unaffected but they live and multiply rapidly in an aqueous solution. In some mammals and in frogs the venom produces a considerable

diminution in the number of blood corpuscles, rapid abolition of muscular contractility with paralysis, sensation however persisting.

By daily injections of increasing doses of salamandrine, commencing with a non-lethal one, an animal can be rendered immune so that it is unaffected by an amount which would prove fatal to an untreated animal. For example, Phisalix (18) gave a young dog weighing 2 kilograms subcutaneous injections increasing from a $\frac{1}{4}$ of a milligram up to 4 milligrams during a month without producing any ill effect. A control animal weighing $2\frac{1}{3}$ kilograms was then injected with 4 milligrams and died at the end of twenty-four hours with the characteristic symptoms.

Another fact of interest is that with both the toad and salamander the venom is fatal to the animal which secretes it only in comparatively large amounts. Thus the last-named author found the lethal dose of salamandrine for the salamander to be from 5 to 10 milligrams subcutaneously, that is a dose from 50 to a 100 times greater than suffices to destroy a mouse. Vulpian (9) made a similar observation with regard to the toad and ascertained that the venom of each of the various species is toxic to the remaining species, though all have a general similarity in action—for instance salamandrine is fatal to toads and tritons in ordinary doses, the venom of the toad is fatal to tritons and *vice versâ*, while the venoms of the toad and triton poison the salamander (21).

The secretory apparatus of the venom glands is governed by a nervous mechanism, the centres for which are located in the optic lobes as was shown by Phisalix and Contejean (22). Muscarine, strychnine and ammonia excite secretion, while cocaine, eserine, and morphine inhibit it. It was incidentally noticed that the salamander is remarkably refractory to certain poisons, it is only completely curarised by 43 milligrams of curare while morphine is apparently quite inactive. The interesting fact was demonstrated that the salamander's blood and blood-serum act as an "antitoxin" towards curare (23). The following experiments illustrate this—20 parts of the defibrinated blood were mixed with $1\frac{1}{2}$ parts of a 1

in 1000 solution of curare and injected into the peritoneum of a frog, while as a control 20 parts of salt solution mixed with the same amount of curare were injected into another frog, this latter was completely curarised in ten minutes, while the former one was unaffected. In other experiments the serum was first injected into frogs and the curare subsequently. Thus a frog received 1·3 c.c. of serum and the following day 0·39 milligram of curare, six times the lethal dose, without showing any symptoms. It was ascertained that 0·4 c.c. of serum just neutralised the minimal fatal dose of curare (mg. 0·065) for the frog.

This summary suffices to show that the belief of the ancients in the venomous nature of the toad and salamander was not altogether devoid of foundation. The appearance of these creatures and the peculiar sensation experienced on handling them, to many most repulsive, together with their shy, retiring habits, would favour an evil repute in an age when Nature was not studied as she is now and before the advance of scientific investigation and the growth of individual culture had banished superstition and ignorance.

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RICHARD T. HEWLETT.

THE RED PIGMENT OF FLOWERING PLANTS.

GREEN is the fundamental note in the colour symphony of plants; but red is of frequent recurrence. The green colour is due to a mixture of pigments called chlorophyll held in the meshes of protoplasmic bodies, capable of growth and division, termed plastids; the red, of the foliage of higher plants, is caused by a colouring matter known indifferently as anthocyan or erythrophyll which is dissolved in the cell sap. With another red pigment, phycoerythrin, which gives the characteristic colour to the group of algæ, the Florideæ, and which is associated with chlorophyll in the plastid, this paper is not concerned.

The part played by the green pigment chlorophyll in the economy of plants is well known; but the *rôle* of the red colouring matter is obscure and the subject of much guess-work. Since, however, some experimental researches have recently been directed to the elucidation of the question, it seems not inopportune here to summarise what is known concerning the properties of this red colouring matter.

The colouring matters, soluble in water, which are contained dissolved in the cell sap of many plants are, by some, termed collectively anthocyan, or, more objectionably, erythrophyll (1); by others, they are referred to two groups, the reds, blues and blue-greens to the Anthocyanin or Cyanin (2) group; the yellows and yellow-browns to the Anthochlorin or Xanthëin group. As will be seen, the chemical nature of these pigments is unknown and consequently any complicated terminology premature. Opinion is divided as to whether the red and blue pigments are in reality identical, the respective colours being due to acidity or alkalinity of the cell sap, or whether they are different chemical bodies. Krukenberg, (3) in his comparative

physiology of colours and colour bodies, seems to regard these various pigments as identical, stating that the blue and violet pigments are converted by acids to reds; and the reds by iron sulphate and by sodium phosphate to violet; by saturation with sodium salts to blue; by the action of alkalis, a red solution becomes green and neutralisation by any acid revokes the original red. Hansen (4) too, relying on his spectral analyses of red and blue pigments prepared from various members, believes in the identity of the variously coloured pigments. N. J. C. Müller, (5) on the other hand, claims to show, in the case of flowers, a much greater variety of pigments than is generally thought to exist. He examines the substances in question before treatment with special reagents and after the action of sulphuric acid and of potash. By the action of potash on various red pigments he obtains a series of derivitive colours, blue, blue-green, yellow, brown and green. Müller does not state, however, how his original solutions are obtained; and so at present it must be left doubtful as to whether the red and the violet pigments dissolved in the cell sap, or even the reds from different plants, are of the same or of different chemical composition.

Concerning the origin of these colouring matters, which for convenience may at present be termed collectively anthocyan, our knowledge is a little more exact. In the first place, there seems to be no question that they are *not* derived from chlorophyll. For, not only does red-coloured sap occur in the cells of young tissues before chlorophyll is developed, and also in the cells of various phanerogamic parasites (devoid of chlorophyll) as *Balanophora*, *Rafflesia* and the Hydnoreæ; but also Hansen (6) describes in the leaf parenchyma of species of aloe, a colourless chromogen which, acted on by water and oxygen, gives rise to a red pigment similar to that contained in many fruits. Like chromogens are probably to be found in many of those colourless underground parts of plants, such as the rhizomes of *Dentaria bulbifera*, *Viola* sp., etc., which become violet coloured on exposure to light. Wigand (7) has shown that red sap is peculiarly characteristic of tannin-containing

plants, and that the pigment of this sap arises from a colourless highly refractive substance giving tannin reactions. Kraus and Detmer (8) also hold the view that the reds appearing in the autumnal coloration of leaves, in so far as they are due to substances dissolved in cell sap, also originate from tannins. Pfeffer, (9) on the contrary, states that in no case has this origin been actually proved. Kutscher (10) and more recently Pick (11) claim to have demonstrated the transition from tannin-reacting substance to red pigment in many flowering plants. The latter author describes a large number of cases of developing shoots whose cells, which a little later are filled with red sap, abound in a colourless, refractive, tannin-reacting substance, the disappearance of which is followed *pari passu* by the advent of the red pigment.

It has long been known that external conditions exert an important influence on the production of the red colouring matter. Senebier (12) observed that, in fruits partially covered by tin foil, the red is only developed in the areas exposed to the sun. Von Mohl notes in his *Vermischte Schriften* that the red colour is called forth by illumination, and that a low temperature favours its appearance. Landel (13) has investigated the influence of light more completely, and finds that variations of the intensity of the sun's rays act uniformly, but in varying degrees, on the production of red colours in stems and other parts.

Sachs' (14) classical experiments, by which he found that the colours of flowers are developed in the dark—albeit, according to Askenasy (15), more feebly than in the light—and also the facts that red sap may occur in dark grown and underground parts, indicate, unless we suppose here a prolonged after-effect of light, that external conditions influence the amount of formation rather than the actual formation of the pigment.

It may be well here to enumerate the chief localities in which anthocyan may occur, in order that the intricacy of the problem of its physiological significance may be borne fully in mind. The following is largely based on Frank's classification :—

Temporary Red Coloration.

1. Young developing shoots: common in temperate regions; very characteristic of trees of hill country of tropics.

2. Autumn leaves during depletion.

3. Grown green leaves during cold weather of spring or autumn (red on light-exposed side).

Temporary or Permanent.

4. Stem, leaf-stalk and mid-rib becoming red in sunny places, not in shade.

5. Wounded or weak places of leaves and fruit (neighbouring sound tissue often red).

6. Alpine plants.

7. Plants of deep shade (specially within the tropics).

Permanent.

8. As a phenomenon of variation.

From this summary it will be clear, how grave is the difficulty of ascribing to anthocyan any single consistent function, and how tempting it is to apply the neo-teleology of adaptation to each case. The pursuit of this doctrine of the obvious has been followed by none more keenly than by Kerner (17), who supplies a significance for nearly all the different occurrences of anthocyan. His statements, in some cases supported by experiment, are as follows. To the anthocyan occurring in the under side of leaves, *e.g.*, in floating leaves and those of shady forests, and in the non-chlorophyll containing parts of Alpine plants, he assigns the function of a converter of light to heat, by which means the metabolic processes of the plant may be conceived to be facilitated: transpiration, for example, being augmented. In seedlings, developing in spring or in cold weather, the anthocyan appearing promiscuously in the leaf, but mainly along the veins and on the leaf stalk, assists, according to him, the translocation of carbohydrates by keeping back light which he states to be inimical to this transport. Lastly, the

anthocyan occurring in the upper epidermis of many Alpine plants, and which he finds is the more developed the more intense the light, Kerner regards as a protective screen to chlorophyll.

It is seen then that anthocyan, in its time, plays many parts. The last-mentioned screen theory may be first considered. Kerner supports his view by interesting observations on the growth of plants in Alpine (Tyrol) regions. He finds, for example, that *Satureja hortensis* flourishes at heights of 2195 metres, and he attributes this to its power of forming large quantities of screening anthocyan. Flax, on the other hand, grows well at 1500 metres, but turns yellow and dies at 2195 metres. Could flax manufacture anthocyan like *Satureja*, Kerner adds, it would blossom and fruit like it. Kerner attributes the death of the flax to the destruction of its chlorophyll, which, in the case of Satureja, he assumes to be screened by anthocyan. But this inference is hardly justifiable. It is true that Pringsheim (18) showed long ago that intense artificial light destroyed the green-colouring matter of living plants, and indeed in some cases destroyed the protoplasm itself. Wiesner (19) similarly has brought experimental evidence to show that chlorophyll may be destroyed by too intense sunlight. Other observers have expressed themselves in the same sense (20). Johow (21), for instance, states his belief that the action of light on chlorophyll is indirect, and takes effect especially in young and in shade-loving members. So that although some writers, such as Stahl (22), do not attach great importance to this destroying action of sunlight, it may be conceded that too intense insolation is a source of danger to the plant.

This general truth, if general truth it be, is not sufficient to make Kerner's interpretation of his results justifiable. For Pringsheim (23), and in more recent times Marshall Ward (24), have shown that the destructive action of light commences in the region of the blue-green, and rises to a maximum in the violet. Till the precise spectrum of the pigment in *Satureja* be examined, it cannot be affirmed that this body is capable of acting as an efficient absorbent

medium for the toxic rays. It may be confidently stated that ordinary anthocyan obtained from various plants would be by no means serviceable in this respect, as the curves of anthocyan absorption figured by Engelmann show, and as will be readily understood when the absorption spectrum of anthocyan is later described. It is true that violet cell-sap absorbs more of the violet end of the spectrum than does red-coloured anthocyan, but even this colouring matter intercepts still more of the red end of the spectrum than of that rich in toxic rays.

The screen theory must then, for the present, be regarded as non-proven. Stahl has criticised Kerner's view very adversely. He inclines to the belief that too much weight has been attributed to the destructive effect of light on chlorophyll; whereas the thermal effects, helpful or harmful, have not received sufficient attention. He adds the further criticism that, before Kerner's conclusions from his Alpine experiments can be accepted, other researches must be made, some at still higher altitudes, others in which some of the plants are protected at night; for as will be seen when Stahl's own work is considered, the death of the Linum plants may be due to a cause other than that of too intense light. The consideration of the other two of Kerner's conjectures concerning the functions of anthocyan may be postponed till the researches, in which they are respectively re-stated are discussed.

The absorption spectrum of the red-colouring matter of leaves has been very fully investigated by Engelmann (25). He finds a general agreement in this respect between the red pigments of different plants. The absorption by these red pigments is greatest in the green but extends as far as the D line on the one side and beyond F, although here very feeble, on the other; beyond G again there is some little absorption. Thus the absorption spectrum of anthocyan is practically the reciprocal of that of chlorophyll. Engelmann remarks that in many plants the chlorophyll grains live permanently behind red screens of such absorbent power that $\frac{1}{3}$ to $\frac{1}{2}$ of the total light is absorbed, without assimilation being in the least impaired.

In passing, it is interesting to note that Engelmann sees in these facts a confirmation of his important assertion that the amount of assimilation effected by light of a certain wave-length is proportional to the degree in which that wave-length is absorbed by chlorophyll; and he draws attention to the fact that the above observations do not so well fit in with the older view that the maximum assimilation is effected by yellow light, in as much as anthocyan effects some considerable absorption of that light. As to the positive significance of anthocyan, Engelmann is silent.

A paper by Pick (26), dealing specially with the significance of the red-colouring matter of Phanerogams, has given rise to much discussion. This author confirms Engelmann as to the absorption spectrum of anthocyan and finds that the nearest approach to a substitute for the red sap is afforded by a solution of alum-carmine and next by ruby glass. Pick concludes from his experiments that the red colouring matter of leaves has the function of, in the highest degree, facilitating carbohydrate translocation, without interfering with the assimilatory activity of chlorophyll. This function of anthocyan may be conceived to be of great importance. For, from experiments of Sachs (27) and others, it is known that in many plants the amount of carbohydrate manufactured by the leaf during the day is in excess of the amount which diurnally passes as sugar from the leaf. The carbohydrate not immediately translocated takes the form of starch and as such is stored by the leaf. This residue of the carbohydrate manufactured daily is, during the night, converted by diastase into sugar and in this condition passes from the leaf. In places subject to very cold nights this nocturnal work is liable to be both dangerous and ineffectual; dangerous since it may prevent the protoplasm of the leaf from passing into a resting condition when low temperature would do comparatively little harm; ineffectual since at low temperatures translocation goes on more slowly than at higher. Hence the great value of anthocyan, assuming Pick's description of its properties, consists in its power, by

virtue of its absorbent qualities, of pushing forward translocation during the closing hours of the day: in enabling the plant to get a greater part of its work done while it is day.

The most important of Pick's experiments consisted in the study of the starch of assimilation formed by *Ricinus* leaves, and parts of leaves, whilst living behind various screens. He placed, for four hours of the day, the lobes of a leaf of a *Ricinus* plant behind, respectively, 1, ruby glass, 2, orange-coloured glass, 3, watery solution of the sap of red beet-root; whilst the fourth was directly insolated during the time of the experiment. He obtained, omitting those in the case of the lobe behind the orange glass, the following results: The lobe directly insolated contained much starch in its spongy parenchyma but more in the palisade cells; that behind the red-sap solution contained much starch in the conducting spongy tissue and less in the palisade; whilst in that behind ruby glass the starch was almost entirely confined to the spongy parenchyma, only a trace being found in the palisade tissue.

Pick's interpretation of his experiments is, that the lobes behind the red screens had assimilated as well and translocated better than those exposed to white light; and therefore this augmented transport of carbohydrate is due to the light absorbed by the anthocyan.

Wortmann (28) criticises these conclusions very severely, bringing forward the following objections: 1, before these inferences can legitimately be drawn it should be ascertained whether the rays absorbed by the anthocyan can, outside the living cell, increase the activity of diastase, the agent of translocation. Positive evidence at present available shows that this is not so, Detmer having proved that light is without influence on fermentation; 2, the results of Pick's experiments may be explained in quite another way. Wortmann adopts Stahl's suggestion that the palisade parenchyma of a leaf is an adaptation to bright light, the spongy tissue to light of feeble intensity, and thus explains Pick's results: that in bright light the palisade parenchyma will assimilate most actively and starch will appear in its cells;

in feeble light the spongy will appear to advantage as the assimilating tissue, and the greater number of starch grains will then be formed in its cells.

Till Wortmann's objections are rebutted by experiment, Pick's conclusions, that red light, as such, facilitates the translocation of carbohydrate material—and this by increasing the activity of the diastatic ferment—cannot be accepted. Pick's experiments however have to be reckoned with in any attempt to discuss the question of the functions of anthocyan; and it is now to be shown how Stahl harmonises them with experiments of his own and gives to them a simple interpretation.

In an important paper which appeared last year in the *Buitenzorg Annals*, Stahl (29) discusses with considerable fulness this anthocyan question, and brings experimental evidence to show that some of Kerner's hypotheses are, in all probability, correct.

The main fact which he establishes is that members, rich in anthocyan, have peculiar thermal properties, and that these supply the key to the solution of the problem in hand.

Kny (30) had demonstrated that the temperature of the water in a vessel filled with red leaves rose higher than that of water in a similar vessel containing green leaves; and Stahl obtains similar results, using the expressed sap of red-leaved Begonias. By more delicate experiments he fully confirms this heat absorption of anthocyan. In some experiments he uses a delicate thermopyle whose spathulate electrodes can be buried to any required depth in the leaf tissue; in others he measures the rate at which a thin layer of coco-butter melts from the different colour areas of a given particoloured leaf. His sources of heat are, in some cases, a gas burner, in others, a Leslie cube by which dark heat only can be used. In all cases he finds, in red-spotted leaves, that the red areas become warmer than the non-red when the leaf is exposed to a source of light or dark-heat.

These results Stahl applies to the interpretation of various phenomena observed by Kerner and Pick. Thus,

in the case of the Alpine plants Linum and Satureja to which reference has been made, Stahl suggests that the red *Satureja* thrives because its anthocyan enables it to take the fullest advantage of the sun's rays. Owing to it, the leaf reaches a higher temperature than it otherwise would; and, in consequence, its general metabolic processes, not merely those of carbohydrate translocation, are favoured. The flax plants wither because they lack the colouring matter which would enable them to take advantage of any favourable change of temperature. And he observes a fact which, it must be confessed, however, might be taken to have merely a pathological significance, that in flax grown at 1800 metres, after exposure to nights during which the temperature fell to 0°C., the leaves were full of starch. A real difficulty seems to object itself to this simple interpretation: to wit, that, as Stahl shows, tissues containing anthocyan not only become warm more quickly than the ordinary green parts, but that, when the source of heat is removed, they become cool more quickly; and until it be shown that excessive radiation is not a source of danger to such plants as those growing in high altitudes, it must appear at all events possible that what the plant gains by heat absorption during the day it loses, by increased radiation, during the night. Stahl is careful to point out that much of the foregoing is speculative, and contents himself with the statement that, in any case, his view of an acceleration of general metabolic activity by the heat-absorbing anthocyan (erythrophyll) has pressing claims for consideration. Pick's results Stahl explains in a similar way. The anthocyan is of importance not because it brings the red rays to bear on the translocation process in particular, but because by its heat-absorbing properties it furthers "die Stoff- und Kraft-wechsel Processe" of the plant.

The occurrence of anthocyan in very many localities, as for example extrafloral nectaries, the secreting end-cells of glandular hairs and at the foot of many sap-containing hairs is noted by Stahl, who expressly contents himself with pointing out that possibly here the colouring matter may

be of the same general service to metabolism as in the cases already cited. Whether, in the case of extrafloral nectaries, the red may be regarded as a signal to ants, as Schimper (31) has suggested, requires further investigation.

Perhaps a fair picture of how anthocyan may act in such cases as those just mentioned may be sketched as follows. In organs of plants of high metabolic activity tannins are of frequent occurrence. Tannins readily give rise to the colour-bodies whose thermal properties are such as may be conceived to be useful to the plant. External conditions such as intense light and low temperature are sufficient to set up the slight modification in direction of the metabolism of the tannins resulting in the formation of the colour-bodies. The principle of selection leads us to assume that *therefore* the anthocyan is useful: whereas if we followed the principle of experiment a whole series of researches would be required to establish the final proposition: as, for example, what exactly is the normal course of metabolism, how far can external conditions modify it and how is the plant affected when, by appropriate means, we prevent the formation of the anthocyan? In short: the explanation of an adaptation may be brilliant but cannot be sound since it is based on only one of the two scientific methods, deduction and induction. Hence to complete the fair picture just sketched we must add that experiments, to render it probable that the general mode of action of anthocyan consists in increasing metabolism, are still to be made.

Stahl applies his discovery of the considerable heat absorption by anthocyan to the case of anemophilous flowers in which red is the strikingly predominant colour, so much so, indeed, that it has led MacLeod (32) to express a doubt as to whether colours are indeed special adaptations to insect fertilisation.

The wind-fertilised flowers in question are those of many dicotyledonous trees such as the poplar, ash, elm, alder and hazel, and of shrubby plants as *Rumex* and *Poterium*. In such plants, flowering during the uncertain

weather of early spring, the red-colouring matter of the style, by virtue of its heat-absorbing powers, may materially accelerate the growth of the pollen tube toward the ovary and thus minimise the danger to the pollen grain from exposure on an unprotected stigma. Similarly the red colour of various gymnospermous flowers may accelerate their opening.

The deep red colour assumed in Alpine regions by the flowering spikes of various grasses such as *Poa annua* may have a similar significance—Kerner suggests indeed that probably the anthocyan converts "light rays" to heat—. We know that a rapid opening of some grasses is brought about by a quick growth of the anther filaments and that this can be effected by placing the grass spike in the mouth. How far this suggestion, that the heat-absorbing anthocyan favours the opening of flowers at the most propitious season, is capable of application to other brightly coloured Alpine flowers must for the present be left undecided; but, as Stahl remarks, a following up of the question seems likely to bring many interesting facts to light.

Hitherto plants, of more or less temperate regions only, have been considered and we have seen that in these the anthocyan probably functions as an accessory to chlorophyll in the absorption of radiant energy. According to Kerner the energy absorbed is that of the light waves which are converted by the fluorescent colour substance into heat: according to Stahl the heat rays are directly absorbed. The energy so acquired is applied to the accomplishment of the plant's metabolism, especially of the translocatory processes.

We come next to consider the distribution and function of anthocyan in plants of tropical regions.

Stahl points out that anthocyan occurs frequently in shade plants of the tropics, chiefly in the under epidermis, or in the spongy parenchyma of the leaf. In the steaming jungle, where a high temperature uniformly obtains, Stahl sees little need for a means of increase of general metabolism, and consequently casts about to

find some fundamental plant process in need of assistance.

Such a process is transpiration. Experiments made with branches of beech and hazel, bearing, in the case of either plant, red and green leaves respectively, show that the transpiration of the red leaves is greater than that of the green, especially if the branch be not exposed to direct sun, or if it be kept in an atmosphere rich in aqueous vapour; which conditions, it is to be noted, are those imposed by their habitat on shade-loving tropical plants.

Other experiments made with branches bearing red-spotted leaves, *e.g.*, *Polygonum persicaria*, *Maranta Kerchoviana*, in which the cut stalks were placed in eosin solution, showed that the liquid travelled first to the red patches of the leaf, from which it is reasonably inferred that transpiration is greatest in those areas. These experiments are the starting-point for Stahl's most interesting speculations. He recalls Wiesner's (33) discovery that plants in a saturated atmosphere may continue to give off water of transpiration owing to the conversion of light rays by chlorophyll into heat, and a consequent increase in tension of the aqueous vapour of the inter-cellular spaces in the plant above that of the vapour outside. Stahl reasons that anthocyan as a heat absorber may act in a precisely similar way and supplementary to the chlorophyll. Now there is indeed some evidence to show that transpiration of plants within the tropics may, under certain conditions, be very low. Haberlandt (34), whilst in Java, made experiments which gave the remarkable result that transpiration of plants belonging to the middle Europe flora is about half as much in the tropics as it is in their native habitat. Stahl has criticised these experiments adversely. Burgerstein (35) and Wiesner have shown conclusively that Haberlandt's results give a most misleading picture of normal transpiration within the tropics, since he excluded direct sunlight from his plants. Into these matters, however, we need not enter here, since Haberlandt's experiments, *under the conditions of his research*, are undoubtedly

trustworthy. They show that, in diffuse light and in a fairly saturated atmosphere, transpiration even in the high temperature of the tropics may be very low. Now these are the conditions to which the shade-plants are subject, and consequently Stahl's theory, that the anthocyan occurring in the leaves of such plants is of importance in the service of transpiration, seems tenable.

So much for the physiological side of Stahl's research. It remains only to refer to experiments which he conducted with a view to ascertain if any of the bright hues, characteristic of tropical foliage, can be regarded as warning colours. Since the bright colours of many flowers and fruits act as decoys to insects and to birds, it seems *a priori* possible that some of those of leaves may be of the nature of warnings to ward off attack.

Otto Kuntze (36) had, for instance, made the statement that the Javanese plant hedges of a red-leaved plant to warn away wild pigs. Stahl's inquiries, however, led him to conclude that the Javanese choose the colour to please themselves.

The result of experiments on feeding various animals, rabbits, sheep and goats on green and red leaves was that the red does not, to any noteworthy extent, act as a warning colour. In some cases the animals in question certainly preferred the green leaves when quite similar in other respects to the red ; but their prejudice gave way immediately when the red leaves were more tender or in other ways more desirable.

To briefly summarise Stahl's work. There is no good evidence for the screen-theory nor for that of warning leaf-colours. Anthocyan is of importance by virtue of its heat-absorbing properties. In temperate regions the heat so absorbed facilitates translocation and general metabolism, to the shade plants of the tropics it is an assistant to transpiration.

A paper endeavouring to arrive at wide generalisations by examining many of the scattered phenomena of colour to be met with in plants and animals has recently been written by Simroth (37). This author believes that all pigments

occurring in organic nature, both in their genesis and in their physiological, possibly indeed in their physical, significance, arise from a single cause, and go back to a single substance which is amalgamated with the original protoplasm and which in its further development and differentiation follows the simple spectral colours in the order of the rainbow. These be brave 'orts, but the author supports them, at all events to some extent, by many curious observations on colour phenomena, which he arranges, for his purpose, in three categories. First, he considers the psychophysiological evidence of vision. He states that with increasing decomposition of rhodopsin (visual purple) a series of colours is produced, running back to the primitive colour. Second, in a similar sense, he remarks the frequent change of colour in animals removed from shallow to deep water. Certain worms (strudelwurmer) have black-brown eyes in the former, whilst at great depths of the sea the colour is red (38). So, too, the algæ (Florideae) growing at the greatest sea-depths are red. A similar change to red is to be met with in animals and plants at high altitudes. These Simroth interprets, not as phenomena of adaptation, but of reversion. Third, the more complicated colour phenomena are most marked in animals, whereas in plants, whose metabolism is less active, the simpler spectral colours predominate. In plants too a change from yellow to green, from xanthophyll to chlorophyll is consequent on augmented metabolism; a change in the opposite sense marking a falling off of metabolism.

Even here Simroth does not reach the end of his speculative tether. He suggests that the cause of the nature of the primary pigment was either that in the earliest times the atmosphere was more watery and denser and thus let only the red rays through, or that protoplasm could at first only respond to the longer wave-lengths.

For botanists, the chief interest of this paper, the confirmation of the main points of which would naturally require far stronger and more exhaustive evidence than is vouchsafed, lies in the suggestion that in cases where no

adaptive significance can be established we have to do with a reversion to "primitive red".

The net result, to which an inquiry such as that recounted in this review leads, seems to be the exceedingly trite one summed up in the great surgeon's dictum, "Don't think, try!" that it is superlatively necessary in such biological problems as that proposed by this anthocyan to attack by actual experiment: that explanations as ready as they are rough, the formulation of which tends to become a pernicious habit, only obscure the true issues concerned.

Biology, in its modern sense, is the subtlest Physiology, dealing with refinements of fundamental processes, and must if it is to join in the procession of truth, follow in the wake of Physiology and "stand upon the order of its going".

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F. W. KEEBLE.

MEAN VALUES, FOR THE YEARS SPECIFIED, OF THE
LICATIONS ARE RECEIVED

Place.	Latitude.	Longitude.	Year.	Declination.
Pawlowsk	59° 41′ N.	30° 29′ E.	1894	0° 10·5′ E.
Katharinenburg	56° 49′ N.	60° 38′ E.	1894	9° 39·4′ E.
Kasan	55° 47′ N.	49° 8′ E.	1892	7° 30·8′ E.
Copenhagen	55° 41′ N.	12° 34′ E.	1894	10° 41·3′ W.
Stonyhurst	53° 51′ N.	2° 28′ W.	1895	18° 37·8′ W.
Hamburg	53° 34′ N.	10° 3′ E.	1895	11° 42·7′ W.
Wilhelmshaven	53° 32′ N.	8° 9′ E.	1895	12° 52·5′ W.
Potsdam	52° 23′ N.	13° 4′ E.	1895	10° 19·9′ W.
Irkutsk	52° 16′ N.	104° 16′ E.	1894	2° 8·0′ E.
Utrecht	52° 5′ N.	5° 11′ E.	1894	14° 21·1′ W.
Kew	51° 28′ N.	0° 19′ W.	1896	17° 10·8′ W.
Greenwich	51° 28′ N.	0° 0′	1895	16° 57·4′ W.
Uccle (Brussels)	50° 48′ N.	4° 20′ E.	1893	14° 48·7′ W.
Falmouth	50° 9′ N.	5° 5′ W.	1895	18° 54·5′ W.
Prague	50° 5′ N.	14° 25′ E.	1895	9° 31·5′ W.
Parc St. Maur (Paris)	48° 49′ N.	2° 29′ E.	1894	15° 15·2′ W.
Vienna	48° 15′ N.	16° 21′ E.	1894	8° 43·6′ W.
O'Gyalla (near Buda Pesth)	—	—	1894	7° 58·2′ W.
Pola (on Adriatic)	44° 52′ N.	13° 51′ E.	1895	9° 47·0′ W.
Nice	43° 43′ N.	7° 16′ E.	1893	12° 32·7′ W.
Toronto	43° 40′ N.	79° 30′ W.	1895	4° 45·3′ W.
Perpignan	42° 42′ N.	2° 53′ E.	1894	14° 5·7′ W.
Rome	41° 54′ N.	12° 27′ E.	1891	10° 45·1′ W.
Tiflis	41° 43′ N.	44° 48′ E.	1894	1° 43·1′ E.
Madrid	40° 25′ N.	3° 40′ W.	1895	16° 6·6′ W.
Coimbra	40° 12′ N.	8° 25′ W.	1895	17° 42·0′ W.
Washington[1]	38° 55′ N.	77° 4′ W.	1894	3° 39·9′ W.
Lisbon	38° 43′ N.	9° 9′ W.	1895	17° 39·1′ W.
Zi-ka-wei	31° 12′ N.	121° 26′ E.	1894	2° 16·5′ W.
Hong-Kong	22° 18′ N.	114° 10′ E.	1895	0° 27·8′ E.
Colaba	18° 54′ N.	72° 49′ E.	1895	0° 36·9′ E.
Manila	14° 35′ N.	127° 11′ E.	1895	0° 51·6′ E.
Batavia	6° 11′ S.	106° 49′ E.	1894	1° 27·6′ E.
Mauritius	20° 6′ S.	57° 33′ E.	1894	9° 59·4′ W.
Melbourne	37° 50′ S.	144° 58′ E.	1894	8° 13·6′ E.

[1] At new observatory, situated some little distance from old station.

MAGNETIC ELEMENTS AT OBSERVATORIES WHOSE PUB-
AT KEW OBSERVATORY.

Place.	Year.	Inclination.	Horizontal Force, C.G.S. Units.	Vertical Force, C.G.S. Units.
Pawlowsk	1894	70° 43·6′ N.	·16456	·47061
Katharinenburg	1894	70° 40·0′ N.	·17799	·50729
Kasan	1892	68° 36·2′ N.	·18551	·47345
Copenhagen	1894	—	·17373	—
Stonyhurst	1895	68° 59·2′ N.	·17148	·44637
Hamburg	1895	67° 44·3′ N.	·18009	·43994
Wilhelmshaven	1895	67° 54·5′ N.	·17983	·44305
Potsdam	1895	66° 39·8′ N.	·18720	·43392
Irkutsk	1894	70° 10·5′ N.	·20116	·55796
Utrecht [1]	1894	67° 10·1′ N.	·18416	·43737
Kew	1896	67° 22·3′ N.	·18309	·43924
Greenwich [2]	1895	67° 15·9′ N. 67° 14·9′ N.	·18323	·43727 ·43692
Uccle	1893	66° 28·4′ N.	·1877	·4311
Falmouth	1895	67° 0·4′ N.	·18547	·43708
Prague	1895	—	·19834	—
Parc St. Maur	1894	65° 5·2′ N.	·19631	·42264
Vienna	1894	63° 12·1′ N.	·20740	·41061
O'Gyalla	1894	—	·21054	—
Pola	1895	60° 34·0′ N.	·22026	·39038
Nice	1893	60° 26·4′ N.	·22198	·39139
Toronto	1895	74° 34·3′ N.	·16645	·60313
Perpignan	1894	60° 10·4′ N.	·22326	·38943
Rome	1891	58° 4·6′ N.	·2324	·3730
Tiflis	1894	55° 46·9′ N.	·25680	·37761
Coimbra	1895	59° 43·6′ N.	·22581	·38685
Washington	1894	70° 34·3′ N.	·19979	·56646
Lisbon [3]	1895	58° 15·7′ N.	·23344	·37731
Zi-ka-wei	1894	46° 0·7′ N.	·32613	·33785
Hong-Kong	1895	31° 46·6′ N.	·36480	·22589
Colaba	1895	20° 48·5′ N.	·37444	·14230
Manila	1895	16° 49·0′ N.	·37808	·11426
Batavia	1894	29° 13·7′ S.	·36749	·20563
Mauritius	1894	54° 41·6′ S.	·23958	·33829
Melbourne	1894	67° 16·9′ S.	·23426	·55956

[1] The Inclination and Vertical Force are from eye observations at 2 P.M.

[2] Of the two values of the Inclination and Vertical Force, the first is based on observations with 3-inch dip needles only, the second on combined observations with needles of 3, 6, and 9 inches.

[3] New dip needles.

THE POSITION OF SPONGES IN THE ANIMAL KINGDOM.

THERE is no group of animals whose affinities and systematic position have been, from the earliest times to the present day, so much a matter of dispute and uncertainty as in the case of sponges; scarcely any theory can be imagined, possible or impossible, which has not been put forward at some time or other. It will be the object of this paper, not indeed to attempt to add another theory to those already existing, but to discuss the problem of the true nature of sponges in the light of the most recent researches upon the group, in the hope of being able to arrive at a decision in favour of one or the other of the many opposing views. An inquiry of this kind falls naturally into three parts: first, an exposition of the various opinions that have been put forth; secondly, a brief critical discussion of the leading features of sponge organisation and development which are of importance for the question at issue; and, finally, any conclusions which may be drawn from the facts in favour of one or the other theory.

Even as late as the middle of this century, the realm of nature to which sponges belonged, whether animal or vegetable, was still a matter of discussion. We need not, however, trouble ourselves with this controversy, long since laid to rest, but we will concern ourselves only with those theories which assign to sponges some place or other in the animal kingdom; and it will be convenient, in considering the different views that have been expressed, to classify them in order according to the systematic position which they assign to the group. We have then three main classes of theories, each with several subdivisions, according as their authors group sponges (1) as Protozoa, (2) as a distinct phylum descended from the Protozoa but distinct from the Metazoa, and (3) as Metazoa.

I.—THE SPONGES AS PROTOZOA.

The older observers, whose histological technique consisted for the most part of tearing up bits of living sponges with needles, and examining preparations made in this way with microscopes which we should not now consider very first rate, nearly all considered sponges as Protozoa. In their preparations they always saw amœboid cells, which could be observed to move about, and sometimes they saw flagellated cells as well. Hence sponges were regarded as colonial forms of Rhizopods, or as masses of Infusorians, intermediate between amœbæ and monads. The former view, advocated by Perty (1852, p. 185), was advanced by Carter (1848, p. 310), who says of the fresh-water sponges: "The animals of which they are but a congeries are identical with the infusorium Proteus". The second view, put forward by Dujardin (1841, p. 306), is the opinion towards which Lieberkühn (1856, p. 512) was more inclined. Saville Kent (1870, p. 217) also regarded the sponge body as "an agregation of amœbiform animals, building up amongst themselves a common skeletal support," and considers sponges, "in a natural and morphological system of classification, to be ranked as the highest representatives of the Protozoa".

The theory of the Protozoan nature of sponges took an entirely new turn with the discovery by James-Clark (1867) of the collar cells of sponges and their great similarity, amounting almost to identity, with the peculiar class of flagellate Infusorians, named by Saville Kent Choanoflagellata. James-Clark (p. 324) declared the sponges to be simply colonies of Choanoflagellata, and expressed the opinion that the collar cells of the different genera of sponges would be found to resemble the various genera of the collared monads, so that it would be possible to divide the genera of sponges amongst the families of the Choanoflagellata.

Both Carter and Saville Kent were converted to this view, and it may be said that the appearance of James-Clark's memoirs was practically the end of all discussion

as to the Rhizopod affinities of sponges. Carter, however, combined an acquiescence in James-Clark's theory of the Choanoflagellate affinities of sponges with peculiar views of his own as to the relationship of sponges to compound Ascidians. He invented the term "spongozoon" or sponge animal for the collar cell, and in 1872 he says (p. 47): "The spongozoon . . . is *the* animal which constructs the sponges generally". In 1874, discussing the flagellated chambers, or ampullaceous sacs as he termed them, he places under this head-line the query (p. 436), "Haeckel's 'gastrula' when developed *in situ*?" He goes on to remark (p. 438): "At one stage the young Ascidian is almost identical in appearance with the ampullaceous sac, that is, composed of a pavement of cells aggregated into a sac-like form. . . . The development of the ampullaceous sac is arrested, and the cells adapt themselves to that condition which ends in the evolution of a sponge; while the sac and its cells in the development of an Ascidian grow to the evolution of a compound tunicated group." After a comparison of the human ovum and a Protozoon he says: "Hence we see that an organic cell may be at one time one thing, and at another another, arising simply from adaptation to the functions required. Thus the cell or spongozoon of the ampullaceous sac becomes an individualised animal, and the *whole* sac, with its oral and anal apertures, so far like an Ascidian; while the sac with its pavement-lining of cells in the compound tunicated animal, goes on unarrested to produce an Ascidian." And he adds: "To produce the 'adaptation' there must be, of course, a creative or directing power, which being *infinite*, we can never comprehend".

Kent in his *Manual of the Infusoria* (1881, vol. i.) devoted a chapter to the affinities of sponges and argues strongly for classifying them with the Flagellata amongst the Protozoa. Besides the great resemblance of the collar cells to the Choanoflagellata he brings forward other grounds in support of his argument, some of which have not been confirmed, while others have been found erroneous by subsequent observers. His most valuable

contribution to the subject was undoubtedly the discovery of a peculiar form of colonial Choanoflagellates, to which he gave the name *Protospongia*, afterwards corrected by him in his description of the plates to *Proterospongia*, the former name being preoccupied. The interest of this form lies in the fact that it consists for the most part of a structureless jelly in which zooids of different kinds are imbedded; at the exterior are typical Choanoflagellate zooids, which serve for the nutrition and locomotion of the colony; in the interior are found amœboid zooids, which arise by modification and immigration of the Choanoflagellate zooids, and which multiply by binary fission dividing up to form spore masses. Each spore becomes a "simple minute uniflagellate monad" which travels to the surface of the colony and is set free. There is thus formed in the interior of *Proterospongia* a tissue very like the gelatinous parenchyma of sponges, especially of those without a skeleton.

From *Proterospongia* it is easy to understand Kent's idea of the nature of sponges. He regards, in fact, a sponge as consisting also of collar-bearing monads, imbedded in a jelly containing amœboid cells, the latter derived by modification of the collar cells. Those amœboid cells may secrete a skeleton, which is, however, not essential. As in *Proterospongia*, so in sponges, Kent professed to have discovered a sporular method of reproduction of the zooids.

Collar cells according to him (p. 174) retract their flagella and collars, "assume a quiescent or encysted state," and "become resolved into the spore masses". "The sponge body is, by ever-progressing internal spore production, rapidly increased in size" (p. 176). These statements of Kent are not supported by the testimony of any other observer, and it is extremely probable, as Schulze remarks (1885, p. 186), that Kent has mistaken bodies of various kinds, such as spermatozoa, pigment granules, cells containing reserve material, etc., for spore masses. Kent denies the existence of spermatozoa and sexual reproduction altogether in sponges. The supposed ova, according to him (p. 187), are simply retromorphosed collar cells, which

"through coalescence with their fellows attain by degrees the comparatively colossal proportions they present" and then by segmentation produce the larva. The latter he considers not to be a larva in the sense in which the word is used among the Metazoa, but "a motile swarm-gemmule, consisting of a more or less ovate colonial aggregation of typical collared zooids" (p. 183). We shall return later to the question of the larva and its composition. Suffice it for the present to say that Kent draws the conclusion (p. 193) that though sponges form in many ways a transitional group between Protozoa and Metazoa, they nevertheless remain Protozoa in every detail, their position being inseparable from the Choanoflagellata, which in their turn lead back to the simplest flagellate monads.

II.—THE SPONGES NEITHER PROTOZOA NOR METAZOA.

If animals composed, as are sponges, of several kinds of tissues, made up of structurally differentiated cells adapted to various functions, are to be classed as Protozoa on the ground that certain of the cells have a great resemblance to certain forms of Protozoa, then the term loses all meaning and becomes impossible to define. We might as well regard man as a Protozoan colony, on the ground that his leucocytes resemble amœbæ. But that sponges are not Protozoa is no reason for classing them as Metazoa, at least if we use the term Metazoa in a genetic, and not merely a descriptive sense, and mean thereby a group or sub-kingdom descended doubtless from the Protozoa, but through a common ancestor which had advanced beyond the stage of a Protozoan colony. This, the usual conception of the term, renders quite intelligible the idea of the existence of other phyla, which like Metazoa are descended from Protozoa, but along independent lines of descent. Thus some authors who have been unable to entertain the notion that sponges were to be classified as Protozoa, have nevertheless been equally unable to regard them as belonging to the Metazoa.

Bütschli (1883, p. 424) was the first to advocate such an idea, and says: "I am of opinion that the group of sponges is one quite shut off from other Metazoa, which arose quite

independently from the class Choanoflagellata". Sollas, though formerly of a different opinion, came round to the same view and proposed (1888, xcii.-xcv.) the name Parazoa for sponges, as a name of the same genetic and systematic value as Metazoa. He regards the possession of collar cells, as well as certain developmental facts, as distinguishing them from the Cœlenterata, the most primitive Metazoa, which in their turn are distinguished by the possession of nematocysts.

Finally Delage (1892, p. 416) has come to the conclusion on developmental grounds, that "the sponges show a progressive differentiation of their elements; but this differentiation does not take place from the beginning in the sense of germ layers comparable to those of other animals". He thinks they may be descended from Protozoa, "but that they have followed since the beginning an isolated development at the side of the stem of the Cœlenterates and other Metazoa".

III.—THE SPONGES AS METAZOA.

The majority of authors, impressed by many facts of sponge organisation, such as their being composed of differentiated cells and tissues, their sexual reproduction, with ova and spermatozoa, and their development through a free swimming larva composed of distinct germinal layers, have regarded sponges as Metazoa, that is to say as descended from an ancestor which had passed the colonial protozoan stage, and which was common to them and other Metazoa. This does not mean however that the majority of authors are united in their opinions; far from it. We have next to distinguish two different points of view, those who regard sponges as cœlenterates, and those who consider them a phylum of Metazoa distinct from the cœlenterates. It is more convenient to take the latter first.

(*a*) *The Sponges Metazoa but not Cœlenterata.*

If sponges are not cœlenterates, the next question which arises is, are they composed of the same primary germ layers, ectoderm and endoderm, as are cœlenterates and all other Metazoa?

Vosmaer (1887, p. 481) while considering the sponges as Metazoa, but not cœlenterates, prefers to leave the question of the germ layers undecided.

Balfour thought that "the germinal layers of the sponges very probably do not correspond physiologically to the germinal layers of other types" (1885, vol. ii., p. 345) whether or not he regarded them as corresponding genetically, *i.e.* as homologous, is not very clear. The great contradictions which were presented by the facts of sponge development as then known, probably prevented him from expressing a definite opinion, for he hints that there are "strong arguments for regarding the Porifera as a phylum of the Metazoa derived independently from the Protozoa". In his discussion of the development of Sycon however (1879) he certainly seems to regard the two layers of the amphiblastula larva as corresponding to those of other Metazoa, but as becoming reversed in position at the metamorphosis, the "locomotor and respiratory" ciliated cells passing to the interior, the amœboid nutritive cells to the exterior.

Maas (1893) puts forward the view that sponges are derived from two layered Metazoan ancestors composed of ectoderm and endoderm, which have taken on a course of development diverging from all other Metazoa, in that the germ layers have become reversed in position, the true ectoderm being internal in the adult, and the true endoderm external.

Heider (1886, p. 230) considers sponges "true Metazoa, and the two primary layers of this group as really homologous with those of higher types," but they are to be separated from the cœlenterata, and regarded as an independent type. Only the blastula and gastrula stages in development are common to both (p. 233).

Goette (1886) also believes that "in the embryonic development of sponges we meet with the blastulæ and gastrulæ common to all Heteroplastids, as the modified ancestral forms of this group also" (p. 51). He thinks, however, that the apparent contradictions in sponge embryology can only be reconciled on the theory that the

ectoderm disappears, and the entire sponge is built up of endoderm, as he claims to have observed in the development of *Spongilla*. On the other hand, "the cœlenterate nature of sponges or their close relationship with the Cnidaria is not in any way supported by their developmental history".

This theory has been further supported by Goette's pupil, Nöldeke (1894), who comes to the following conclusions (p. 185):—

"(1) Sponges possess a typical gastrula with ectoderm and endoderm, which have the typical relations of position to one another.

"(2) The further development of the germ-layers of sponges does not correspond with that known as typical. The ectoderm undergoes a process of degeneration after fixation of the larva, in consequence of which it takes no share in building up the perfect animal.

"(3) Sponges have no genetic relationship with the rest of the Metazoa anywhere above the gastrula stage."

(*b*) *The Sponges as Cœlenterates.*

This is to a great extent the dominant view of sponge affinities; it is the view to be found in most text-books, and generally held by those who are not themselves experts on the question, a fact doubtless largely due to the great names that endorse this opinion. It must not be supposed, however, that here, any more than among the supporters of other theories, shall we find unity of opinion.

The view that sponges were true cœlenterates was first put forward definitely by Leuckart (1854, p. 472) in the following words: "If we imagine a polyp colony with imperfectly separated individuals, without tentacles, stomachal sac and internal septa, we have, in fact, the image of a sponge with its large 'water canals' opening outwardly".

It was, however, Haeckel who first brought this view into prominence. After his pupil, Miklucho-Maclay, had already (1868, pp. 236, 237) affirmed the common descent of sponges and cœlenterates, Haeckel in 1870 laid down the following thesis: "The sponges are most nearly allied to

the corals of all organisms. Certain sponges differ from certain corals only by a less degree of histological differentiation, and especially by the want of urticating organs. The most essential peculiarity of the organisation of sponges is their nutritive canal system, which is both homologous with, and analogous to, the so-called cœlenteric vascular system, or gastro-vascular apparatus of the Cœlenterata. In the sponges, just as in the corals, and indeed in the Cœlenterata generally, all the different parts of the body originate by differentiation from two primitive simple formative membranes or germ lamellæ, the entoderm and the ectoderm. These two lamellæ originate by differentiation from the originally homogeneous cells which (having been produced by the segmentation of the ovum) compose the spherical body of the ciliated embryo, or of the primitive larva (Planula). From the inner or vegetative germ-lamella, the entoderm, originate the nutritive epithelium of the canal system and the reproductive organs. From the outer or animal germ-lamella, the ectoderm, all the other parts originate" (p. 6). According to Haeckel the absence of nematocysts or urticating organs in sponges and their constant presence in corals, Hydromedusæ, and Ctenophora, is the sole morphological character separating the first class from the last three (p. 7). The mark of a sponge individual is the osculum (p. 8), representing the Cœlenterate mouth. The inhalant pores of sponges find their homologue in the cutaneous pores of corals. "Sponges and corals," he concludes (p. 13), "are near blood relations." From the common ancestor of both, the Protascus, originated as two branchlets the Prosycum, ancestor of sponges, and the Procorallum, ancestor of corals.

These statements of Haeckel's were the cause of a controversy between Kent and Lankester, the former maintaining the Protozoan affinities of sponges, the latter defending Haeckel. "Admitting," says Kent (1870, p. 204), "that . . . there in all probability did exist a something equivalent to Haeckel's hypothetical *Protascus*, and from which the existing stock of sponges and corals has probably been evolved . . . the evidence he brings forward in support of the proposed

intimate relationship of the two groups, as they *now* exist is based rather on affinities of analogy than homology." In reply to this admission, which drew from Haeckel the retort that Kent did not so much as know the difference between homology and analogy, Lankester (1870) pointed out that if the structures common to the two groups be derived by descent from a common ancestor they are homologous. To this Kent made the somewhat weak rejoinder (1870, p. 251) that the admission of Haeckel's Protascus was "meant to carry with it the vaguest possible significance and simply as an acknowledgment of my faith in the doctrine of evolution," and states his belief that "the open sac-like contour of all existing cœlenterates and a few exceptional spongiadæ has probably been arrived at by two very different processes of evolution". Kent further sought to contrast the manner in which sponges secure food by ciliary action, as "a purely mechanical and involuntary force" with the voluntary muscular force exerted by an Actinian in seizing its prey (p. 208), a comparison which, as Lankester remarked, proposes to distinguish the two groups "by psychical manifestations" (p. 87). Lankester points out that in Kent's manner of "viewing" sponges all organisms might be classed as Protozoa, and concludes that the result of Haeckel's arguments will be to cause naturalists to admit the separation of sponges from Protozoa, but that "he will have greater difficulty in getting the association with Cœlenterata, and with Anthozoa in particular, admitted".

In 1872 Eimer published a paper describing thread cells in sponges. Carter (1872) at once pointed out, however, that these thread cells did not belong to the sponge but to symbiotic hydroids living in the sponge tissue, and nematocysts have not since then figured in sponge literature. Haeckel, however, in his monograph of the calcareous sponges, published in the same year, modifies his view of sponge affinities. It is now the hydroids and not the corals with which he tries to compare sponges. He regards the most primitive sponges as related to the most primitive Acalephæ, but "Sponges and Acalephæ are two diverging branches of the Zoophyte stem which have

developed from the common ancestral stem of the Protascus" (1872, vol. i., p. 461). In other words, it is no longer suggested that sponges are a group of the same systematic value as one of the divisions of the cœlenterates, but that they are equivalent in the system to all remaining classes of cœlenterates put together. Since Eimer had found nematocysts in sponges their possession is no longer to be regarded as characteristic of cœlenterates, but a distinctive feature of the two groups is the formation of pores in sponges, since he now admits that the cutaneous pores of acalephs are analogous and not homologous with those of sponges; as Kent had already declared to be the case.

Finally, in 1889 (p. 90), Haeckel came to regard the flagellated chamber as the primitive individual in sponges, "homologous with a Gastræa on the one hand and with a simple Hydroid on the other," and concludes: "The position of sponges in the animal kingdom as a separate phylum of the Cœlenterata . . . seems to be the most natural".

The change of position with regard to the cœlenterate theory of sponges which we see in comparing Haeckel's earlier and later writings, finds a parallel in the different stand-points taken by the authors who also support this theory. Marshall alone takes an extreme view similar to that in Haeckel's earlier works, and considers (1885) sponges true cœlenterates descended from a protactinia with tentacles and a radiate gastrovascular apparatus, which persists as the canal system. All other advocates of the cœlenterate nature of sponges take rather the view which may be said to dominate in the text-book and the lecture room, that the Cœlenterata are to be divided into two distinct and opposed groups, the Porifera or sponges, and the Cnidaria or polyps and medusæ. Schulze, whose opinion carries more weight than that of any other authority, after remarking on the similarity of sponge and cœlenterate larvæ, points out that the metamorphosis indicates the point at which a separation took place in phylogeny, but finds it difficult to determine what degree of organisation was reached before the separation took place. He considers, however, that there is very little to sup-

port Marshall's views, and thinks it probable that the oldest sponges had no radial diverticula of their central cavity but a simple sac-like form, like an Olynthus among the Ascons (1885, p. 191).[1]

I have left to the last the peculiar view expressed by von Lendenfeld, since it cannot be assigned a place in the classification of the sponge theories which I have adopted. In his *Monograph of the Horny Sponges* (1889) he compares sponges as "Mesodermalia" with other cœlenterates or "Epithelaria". Facing p. 885 he gives a figure of a tree, representing the pedigree of sponges and other animals. From a massive stem labelled "Protista" comes off a thick branch on the right, labelled at its origin "Animalia," and a little higher up, but before it has divided, "Cœlentera". Just above where this latter name is affixed come off two branches, Epithelaria and Mesodermalia. So far everything seems quite clear, especially when we read on p. 887 that the sponges form "a separate phylum in the *grade* Cœlentera of the Metazoa". But on p. 886 we read that: "The sponges have probably been developed independently of other Metazoa from Protozoan ancestors, the nearest existing relations to which are the Choanoflagellata," and that "the mode of the phylogenetic development of sponges was similar to that of other Metazoa". In spite of this view, however, the author "does not see that there is any justification for the establishment of a special sub-kingdom for the sponges. They are evidently Metazoa and no doubt Cœlentera in the sense given above, namely, the *grade* Cœlentera as opposed to the *grade* Cœlomata" (p. 888). This method of reconciling statements apparently so contradictory as that on the one hand sponges are Cœlenterates, and on the other hand separately descended from the Choanoflagellata, implies a conception of the animal kingdom essentially different from that of all the other authors

[1] Chun, who discusses the question of sponge affinities from the standpoint of a specialist upon Cœlenterata, may be referred to as one who, taking a high rank as an authority upon a group of animals other than sponges, supports the theory of their cœlenterate nature. See Brown's *Klassen und Ordnungen d. T.*, Bd. ii., Abth. 2 (Cœlenterata), pp. 86-96.

whose views we have been discussing, though the theory of a separate choanoflagellate ancestry for a class of cœlenterates reminds one strongly of Kent's admission of a Protascus ancestor for both corals and a class of Protozoa. Doubtless, however, this admission on the part of Lendenfeld was also meant to carry with it the vaguest possible significance and simply as an acknowledgment of his faith in the doctrine of evolution.

From the above exposition of the various theories that have been held as to the nature of sponges, it will be seen that it would be difficult to bring forward a new and original opinion on this subject. No one has yet sought to prove that sponges are degenerate molluscs, arthropods or worms, or that they are the progenitors of Vertebrates, and there is undoubtedly an opening for a physiologist to find the ancestor of sponges in the king crab. Also the theory of Goette that sponges are made up of endoderm alone, suggests a counter hypothesis that they are composed of ectoderm alone. When these two classes of speculations have been brought forward there will remain, so far as I can see, absolutely no new theory of sponge affinities to be propounded.

I propose now to discuss shortly the leading characteristics of sponges and the evidence they afford in favour of, or against, one or other of the above theories. Even if it be not possible at present to arrive at a conclusion as to the true nature of sponges, it may be at least possible to demolish and eliminate some of the numerous theories that have been put forward, and so narrow the field of inquiry. And at the outset it must be repeated that the Protozoan nature of sponges cannot now-a-days be seriously discussed. We have to consider whether sponges have, or have not, a common descent with the Metazoa, and if this question be answered in the affirmative, then whether and to what degree they are or are not cœlenterates. Perhaps the most striking feature of sponges as compared with other animals, is to be found in their peculiar "collar cells". In the lowest sponges, the Ascons, the collar cells form a con-

tinuous layer lining the whole interior with the exception of a narrow rim round the opening of the osculum, where they are absent. In other sponges the collar cells form a discontinuous layer, being confined to certain parts of the canal system, the flagellated chambers. But however distributed they are never absent, at least not so in any sponge that has been properly examined. Not only are the collar cells a constant peculiarity of sponge structure, but they also occur nowhere else in the animal kingdom except in the case of the Choanoflagellata, where we meet with them as separate individuals leading a free existence, sometimes isolated, sometimes united to form colonies, but in no case losing their distinct individuality.

The agreement in form and appearance between the columnar collar cells with their long single flagellum surrounded by the delicate protoplasmic, retractile collar, and the individuals of the Choanoflagellata, is very striking. The variations in the size, form, and appearance of the collar cells in different sponges, are not greater than the variations found amongst the species of Choanoflagellata, if indeed they are as great. The physiological similarity seems to be on a par with the structural resemblance. It is certain that the collar cells take up food particles, and it is probable that this is effected in the same manner as in the case of the Choanoflagellata, namely, through the particles being swept by the flagellum into or upon the collar. Polejaeff (1883, p. 15) has tried to show that the collar cells are not fitted for capturing food particles on the ground that the lashing movements of the flagellum would tend to drive the particles away; but any one who has observed the action of the flagellum in the free Flagellates knows that it is exerted in a manner which would not have this effect. An Euglena, for instance, when swimming has its flagellum in front, and the body is dragged after it, as it were; if now an animal so moving were held fast by its tail and fixed in one spot, as are the Choanoflagellata and the collar cells of sponges, the consequence of the movements of the flagellum would be to direct a current of water towards the base of the flagellum, that is into the

cavity of the collar. In sponges in addition to the currents of this kind produced by each flagellum, there is the main current flowing through the canals and produced by the united action of all the flagella acting together. If this general current be considered alone in relation to the collar cells, it is evident that as it flows past the openings of the collars, each of the cup-shaped cavities which they contain forms a side eddy to the general current, and particles passing near the collars will tend to be carried into them and whirled about inside them by the eddy in their interior, until they come into contact with, and stick to, the protoplasm either of the collar itself, or of the cell at the base. Hence, taking into consideration both the effect of the collars in forming side eddies to the general current, and the manner in which the movements of the flagellum tend to sweep particles into the cavity of the collar, it is impossible to agree with Polejaeff that the collar cells are not suited for ingesting food; on the contrary they must be regarded as eminently well-fitted for a function which repeated experiments have shown them to exercise.[1]

While there is thus a close agreement between collar cells and Choanoflagellata in their general structure and functions, some details are still open to dispute. In the first place there is the question of contractile vacuoles; those authors who especially maintain the Protozoan nature of sponges, namely, Carter, Kent, and James-Clark, all assert the existence of pulsating vacuoles like those of Protozoa, and usually two in number, in the collar cell. These statements are not, however, confirmed by other authors, and though the protoplasm of the collar cells is undoubtedly very vacuolated in a number of instances, it is not certain that any of these vacuoles are contractile. Schulze (1885, p. 180) found the contractile vacuoles to be by no means so regular in their occurrence as usually alleged. Bidder (1895) makes no mention of them in his detailed account of the collar cells of Heterocœla. And the figure given of them by Kent in *Clathrina coriacea* (1881, pl. x., fig. 2) is certainly wrong, since he figures two

[1] Compare von Lendenfeld, *Zeitschr. f. wiss. Zool*, xlviii., p. 674.

vacuoles at the base of the cell and the nucleus in the upper portion, but as a matter of fact in this species the nucleus is at the base of the cell and any vacuoles that occur are lodged in the upper portion. Hence the alleged occurrence of contractile vacuoles in collar cells requires further confirmation before such vacuoles can be regarded as constant features of the cells. A second point with reference to the collar cells is their multiplication. We have already noticed Kent's statement to the effect that they multiply by means of spores. He also asserts that the ciliated chambers develop from "the segmentation of a primitive amœboid body produced . . . by the coalescence of more or fewer metamorphosed collared zooids". These assertions, so far as they have been noticed by subsequent observers, have generally been regarded as erroneous and without value. The fact remains, however, that both the multiplication of collar cells, and the formation of new ciliated chambers, in a growing sponge, are scarcely known, and no satisfactory observations have been recorded with reference to this point. Nevertheless the similarity of collar cells and Choanoflagellata remains a very striking fact, and furnishes the strongest argument, not only for those who seek to class sponges as Protozoa, but also for the authors who look upon them as descended from Protozoa independently of the Metazoa. Those, on the other hand, who regard sponges as Metazoa are obliged to explain the collar cells as secondarily acquired. Schulze (1885, p. 190) considers that the independent origin of collars in the cells of sponges is by no means impossible, since protoplasmic processes and membranes of various kind are of common occurrence in Protozoa. It would, however, have been more to the point to prove that similar structures occur among Metazoa.

While the collar cells have furnished the strongest argument for separating sponges from Metazoa, the peculiar canal system of sponges is a feature which, as may be seen from the opinions quoted above, has very often been used on the other side, especially by the advocates of the cœlenterate theory. Not only was the central gastral cavity of

sponges regarded as an archenteron, lined by a true endoderm, but by the extreme cœlenterists the osculum was homologised with the cœlenterate mouth, and the system of inhalant and exhalant canals with the cœlenterate gastrovascular apparatus. It was soon established, however, that the sponge larva attached itself by what had to be considered, on the gastrula theory, as the blastopore, and hence the homology of osculum and mouth had to be given up.

It is not necessary to discuss further here the alleged homology of gastral cavity and stomach (archenteron), since it will be seen when we discuss the development that such a homology is now quite untenable. One side issue may however be noticed, since it is one that has contributed greatly to confuse the morphology of sponges. In a simple Ascon the internal cavity is lined by collar cells everywhere except at the oscular rim. On the theory that the gastral cavity represents the archenteron, we have in these simplest types the "endoderm" represented by a uniform layer of collar cells. In a Sycon, however, or any sponge above an Ascon, the collar cell layer is discontinuous and confined to the chambers, all the rest of the canal system being lined by flattened epithelium. But an archenteron cannot be imagined as lined by anything else but endoderm. Hence some part at least of the flattened epithelium lining the canal system had to be considered as endoderm, in spite of the fact that it could not be distinguished by any feature whatsoever from the flat "ectodermal" epithelium on the outer surface of the sponge. The exact limits of the "ectoderm" and "endoderm" in the interior of the canal system were much disputed, but the opinion expressed by Schulze (1880, p. 438) generally prevailed, according to which the endoderm furnished not only the collar cells of the chambers, but also the flat epithelium lining the excurrent system from the chambers to the oscular opening, while the ectoderm furnished the flat epithelium covering the outer surface of the sponge and all the incurrent canals up to the chamber pores. It followed therefore that an endoderm consisting primitively of a uniform layer of collar

cells became in part transformed into flat epithelium, and in Sycons, which start developmentally from an Ascon-like condition, this transformation must be continually occurring during growth. If, however, we examine the grounds other than theoretical upon which was founded this theory of the transformation, alleged to be of such frequent occurrence, of collared into flat epithelium, we find direct evidence of any kind, whether histological or embryological, to be entirely lacking. As is shown in the figures published by all trustworthy observers, and especially in those of Schulze, and as can be seen in any good preparations of sponge histology, the collar cells lining flagellated chambers or radial tubes always pass abruptly and without the slightest gradation into the flattened epithelium of the incurrent or excurrent canals. This was especially well shown by Schulze (1875) in his investigations upon just the very sponge in which direct evidence of the modification of collar cells into flattened cells might be expected to be forthcoming, namely, *Sycon raphanus*. Cells intermediate in form between the two kinds of epithelium do not occur, and the many figures of such transitions given by Lendenfeld must be characterised as erroneous. The fact, sufficiently obvious in itself, that a collar cell if cut obliquely may present in sections the appearance of a rounded or columnar cell without flagellum or collar, perhaps will account for some of these incorrect descriptions, though the considerable differences both in the structure of the nucleus and the nature of the cytoplasm between collar cells and flat epithelium cells ought to have been sufficient to prevent any such confusion.

Schulze was led by his observations upon *Sycon raphanus* (1875, p. 258) to regard the flat epithelium as a layer of uniform nature throughout, on account of its great similarity, amounting to identity, both at the outer surface of the body and in the interior of the canal system. His embryological investigations upon Plakina (1880) first led him to express the contrary view referred to above. It cannot, however, be said that his figures of the latter form afford any direct evidence of an "endodermal" flat

epithelium. A stage showing the internal cavity of the young sponge lined by columnar cells is compared with a later stage in which flagellated chambers open into a gastral cavity lined by flat epithelium. From the comparison it is inferred that the flat epithelium of the gastral cavity owes its origin to a flattening of the columnar "endoderm" cells. Two other inferences, however, are just as possible, either that the lining of flat epithelium originates by an exposure towards the gastral cavity of the outer germinal layer when the "endoderm" is aggregated into the chambers, or that the columnar cells of the earlier stage are not all "endoderm".[1] In any case *Plakina* is, like *Halisarca*, one of the forms which requires renewed investigation, the facts of its development as at present recorded standing in irreconcilable contrast with the development of other forms.

It must therefore be granted that, with all the respect deservedly due to so great an authority, Schulze has not brought forward absolutely convincing proof of the origin of the internal flattened epithelium by modification of the collared gastral layer. On the other hand such direct embryological evidence as exists with reference to the origin of the flat epithelium of the interior shows it to be derived from the *dermal* layer, the inner cell mass of the larva. Both Maas (1892 and 1893) and Delage (1892) are united upon this point, and agreed that the ciliated layer of the larva furnishes the chambers, and nothing else. To establish what may be termed *the continuity of the ciliated cells* is, as we shall see, the tendency of recent investigations upon sponge embryology; that is to say, the ciliated cells of the larva become the ciliated cells of the adult, in spite of the very great changes in position this implies, and nothing else is formed from them. In other words, the gastral layer when once differentiated remains uniform in nature throughout the life cycle.

Nothing is more difficult than to establish a negative, and the above conclusion as to the uniformity of the gastral layer would be at once upset if it were shown clearly and in a trustworthy manner that in any single case collar cells are

[1] Compare Maas (1893), pp. 423, 424.

transformed into flattened cells. For the present I think, however, we are justified in regarding the notion as one of the many assumptions which, founded on a mistaken theoretical basis, and opposed rather than supported by the facts, have dominated and falsified sponge morphology.

The physiology of sponges, so far as it is known, does not present much analogy with the Metazoa generally, or with cœlenterates in particular. Although much is uncertain or unknown, three things are fairly established. First, that the osculum is always an exhalant opening, from which issue forth the currents which enter at the pores and stream along the canals. Secondly, that ingestion may be performed by either layer. Numerous experiments by Lieberkühn, Metschnikoff and others, have shown beyond all doubt the capacity of the collar cells to take up small food particles from the water which apparently they transfer to the amœboid cells. On the other hand Metschnikoff (1879) showed clearly that in some sponges (*Reniera*) the food particles are ingested by cells in the dermal layer, and his observations have been confirmed and extended by subsequent investigations.[1] Metschnikoff also confirmed the observation of Lieberkühn (1857, p. 388) to the effect that in *Spongilla*, Infusoria carried in by the current through the pores into the subdermal spaces and inhalant canals were absorbed there by the wandering cells; a fact which helps to explain the great development of the inhalant canal system in higher sponges, and throws light on the superior benefit derived by the sponge from the more complicated canal systems as compared with simpler forms such as the Ascons, which are probably capable only of ingesting microscopic particles by means of their collar cells. A third principle of sponge physiology is that all digestion is intracellular, and apparently performed by the wandering amœbocytes, the "cellules digestives pigmentées" of Topsent. So far, therefore, as conclusions can be drawn from the physiology,

[1] *E.g.*, by Lendenfeld in *Aplysilla violacea* (über Coelenteralen der Südsee II., etc., *Zeitschr. f. wiss. Zool.* xxxviii., 1883, p. 252); but in his more recent work (*ib.*, xlviii., 1889, p. 674) he goes back upon his former opinion.

it presents us with a more primitive, less specialised condition than we find in the Metazoa *sensu strictiori.*

The reproduction of sponges on the other hand is of a distinctly Metazoan type, by means of true ova and spermatozoa. This is a fact which has been called in question at various times, but, without entering into a detailed discussion, it must be regarded as established now beyond the possibility of doubt, in view of the accurate observations of Schulze upon various types of sponges, Fiedler (1888) upon *Spongilla*, and many other authors. Their evidence is in no whit invalidated by the fact that many of the descriptions of supposed spermatozoa relate in all probability merely to ordinary flagellated cells. On the other hand, full and detailed accounts of the phenomena of the growth and maturation of the ovum in different types are much to be desired. The only such account existing is that given by Fiedler (1888) with reference to the ovum of *Spongilla*, which shows some remarkable deviations from the type usually considered as the normal for Metazoa. The polar bodies, for instance, do not originate by a karyokinetic division of the nucleus of the ovum, but are, as it were, budded off after disappearance of the nuclear membrane from the large spherical chromatin mass occupying the centre of the vesicular nucleus. They arise, therefore, by a process more akin to direct division, and a quite similar process, only differing in that the central chromatin mass divides into equal halves within the still present nuclear membrane, occurs at each division of the nucleus during the segmentation of the ovum. The absence of karyokinesis in processes where its occurrence is usually so constant is the more remarkable when it is seen that true and typical mitoses are found in the tissue cells and the spermatogenesis of *Spongilla.* Not only are more observations upon other forms much needed, but the details of the fertilisation of the ovum are quite unknown in any sponge and remain for description.

Some authors have regarded the ovum of sponges as an asexual reproductive body made up of a fusion of cells. We have noticed already Kent's statement that the ovum

is produced by a fusion of retromorphosed collar cells. Goette (1886) also believed the ovum of *Spongilla* to be multicellular in nature, but his descriptions have been shown very clearly by Fiedler to be erroneous. More recently, H. V. Wilson (1894, pp. 285-294 and 327-329) regards the reproductive body from which the larva arises as in some cases a gemmule produced by cell fusion, in other cases as a true ovum (*Tedanione*, pp. 341-343). That an essentially similar free-swimming embryo should be in one case a true larva produced from a fertilised ovum, and in another case "a bud embryo exhibiting ancestral traits," derived from an asexual gemmule, is a state of things which would require very convincing proof before it could be accepted. It seems, however, far more probable that Wilson's statements, and also, we may add, those of Kent, rest as Maas suggests (1896, p. 233) upon a mistaken interpretation of a process of oögenesis.

The last feature of sponge organisation which we need discuss, namely, their embryonic development, is perhaps the most important of all when considering the question of their affinities. The ontogeny alone enables us to decide how far the resemblances between the adult forms of sponges and other animals are due to a similar origin, or are secondarily and independently acquired; in other words, to distinguish between what is homologous and what is analogous. And just as the reproduction seems to be of a distinctly Metazoan type, so also may be said of the earlier developmental history. The segmentation of the ovum presents no special features and may be described as total and regular. It results typically in a blastula of the usual type, from which the diblastula, or two-layered embryonic condition, arises in different forms in a variety of ways, all of them, however, paralleled in other groups of Metazoa. In the lower Ascons, in *Halisarca*, and in *Plakina*, it is formed just as in many Hydroids, by an immigration of cells either at any point or from the posterior pole. A simple modification of the latter type leads to the amphiblastula larva, the only larval form at all specially characteristic of sponges where the cavity is too small to contain the immigrated

cells which therefore protrude posteriorly (Minchin, 1896). In *Oscarella* the two-layered condition is formed by a simple invagination. Finally in the highly specialised Cornacuspongiæ the segmentation results in a solid morula or sterroblastula, and the two embryonic layers are differentiated *in situ*. In whatever way the two layers arise, the result is a two-layered larva presenting in most cases striking resemblances to the cœlenterate planula. It consists of an external ciliated layer more or less completely surrounding an internal mass of amœboid, granular, non-ciliated cells. When food yolk is present in any quantity it is contained in the cells of the inner mass. Hence in this point as well as in their relative position and general characteristics, the outer and inner layers of the sponge larva are quite similar to the ectoderm and endoderm of Cœlenterata and other Metazoa.

So far the way is clear, and the facts are scarcely disputed, even by advocates of the most opposed views. It is the metamorphosis of the simple sponge larva, that is to say, the fate of its component layers, and the part they take in building up the adult sponge, which is the important question to decide.

Before proceeding, however, to discuss this question it is necessary to be clear as to the terminology we employ for the cell layers under consideration. The words ectoderm, mesoderm, and endoderm, have been universally employed in sponges, sometimes in a purely descriptive sense, but more often as implying a homology with the similarly named layers in cœlenterates. Not only is such a homology more than doubtful, but even in a descriptive sense the use of these terms is in the highest degree confusing and misleading. For in the larva the ciliated layer has been termed the ectoderm, and the inner mass the endoderm or endo-mesoderm, while in the adult the term ectoderm has been applied to the external, and more or less of the internal epithelium, the term endoderm to the rest of the internal epithelium, and the term mesoderm to all the tissue enclosed between the epithelia. It is, however, far from certain, and indeed highly improbable, that the similarly named layers

of the larva and adult correspond, and a terminology which implies any such correspondence is to be avoided. Both for these reasons, and on account of the homologies implied by the words "ectoderm," "mesoderm" and "endoderm," I have proposed to revive for the layers of the adult sponge the purely descriptive terms originally coined by Haeckel (1872, vol. i., p. 130), namely, the term "gastral layer" to denote the internal collared epithelium and the term "dermal layer," to denote the remaining tissues. Thus the gastral layer corresponds in Ascons to the whole of the "endoderm" of authors and in other sponges to a part of it; the dermal layer is the "exoderm" of Haeckel, the "ectoderm" with the "mesoderm," and sometimes part of the endoderm of other authors.

The larva, as we have seen, consists of an external ciliated layer and an inner cell mass. How do these layers correspond with the layers of the adult? Which of the two layers of the larva is "gastral" and which is "dermal"?

In a former number of this journal (1894) I discussed the question of the relation of the layers of the sponge larva to those of the adult at some length, especially with references to the works of Maas (1892 and 1893) and Delage (1892). I showed that the works of these two authors, differing much in respect to details, but agreeing on the points of fundamental importance, rendered it possible for the first time to treat the embryonic development of sponges generally from a uniform and reasonable stand-point. Both authors, in fact, agreed in affirming that, contrary to the usual belief, the ciliated layer of the larva of Cornacuspongiæ passed into the interior at the metamorphosis and became the gastral layer of the adult, that is to say, the collar cells of the chambers, while the inner mass of the larva gave rise to the remaining tissues of the sponge, namely, to the flat epithelium lining the exterior and the incurrent and excurrent canals, and the whole of the so-called mesoderm, in other words to the dermal layer as here defined. Thus it became at last possible to reconcile the apparent contradictions resulting from a comparison between the well-known development of *Sycon* and that of other sponges. There remained however certain cases

where the development required re-examination in the light of these views, in order to determine whether a similar reversion of the layers, not hitherto suspected, did occur, or whether the recorded statements were correct. These cases were, besides *Oscarella* with its somewhat peculiar development, *Plakina*, *Halisarca*, and the Ascons.

Since my review of these questions in this journal, three works have been published upon sponge development, those of H. V. Wilson (1894), Nöldeke (1894), and myself (1896). To take the last first, I have shown that in the Ascons the layers become reversed in a manner similar to that described by Maas and Delage, and that it thus becomes possible to homologise the parenchymula and amphiblastula types of development, the internal non-ciliated cell mass of the former being homologous with the posterior non-ciliated cells of the latter, and giving rise in the same way to the dermal layer of the adult.

The observations of Wilson on the other hand, dealing with several species of Monaxonida are interpreted by him in an opposite sense to the views expressed by Delage and Maas after a study of the same class of objects. Wilson believes that the ciliated layer of the larva becomes the "ectoderm," that is to say the dermal layer of the adult, and derives the collar cells, the "endoderm," from the inner cell mass of the larva. He thus brings us back once more to the old views of sponge embryology, which sought in vain to construct a uniform type of sponge development from a chaos of contradictory and irreconcileable observations.

Not only must I confess myself biassed against Wilson's views on general grounds, that is to say, on account of the impossibility of homologising in any other way the amphiblastula and, I may add, parenchymula larva with other types; not only am I greatly inclined to regard Wilson's statements as less convincing than those of Maas and Delage; but I consider that Wilson's own recorded observations are not at all in harmony with his interpretations of them. Wilson has objected strongly to his figures being taken as evidence against his views, a somewhat curious position to take up if his figures profess to be accurate; we can

but criticise what he puts before us. I must therefore venture to point out that he has figured in the plainest manner the immigration of the ciliated cells, and the formation of the chambers from them. On plate xvi., figs. 26, 27 and 28, show in surface view the growth of the inner mass over the ciliated cells; in fig. 30 we see the ciliated cells heaped up at one pole and becoming internal: figs. 39, 40 and 41 of plate xvii. show groups of these cells forming chambers, though their cell outlines are not represented; and figs. 44, 45, 47 (plate xviii.) and 50, show later stages with chambers formed of cells with small nuclei, similar to the larval ciliated cells. On plate xvii., again, fig. 36 shows some of the ciliated cells not yet absorbed, others scattered through the interior, and even arranged to form chambers, and figs. 38 and 43 represent later stages in which the chambers are well shown to be formed from the small cells. Finally attention must be drawn to the most important stage figured on plate xxi., fig. 85, showing in a larva just fixed the commencing inversion of the layers. Knowing how easy it is to represent in drawings what one believes the preparations to show, it is remarkable to find in Wilson's figures so much evidence for a view opposed to that which he holds, and the fact is certainly a great testimony to the accuracy of the author's observations. Wilson does not always represent the disproportion in size between the nuclei of the two layers as distinctly as has been done by Maas and Delage, no doubt because the point never occurred to him as one of importance. While, therefore, Wilson's figures must be cited as a most valuable contribution to the theory—or rather the facts—of the inversion of the layers, it may further be pointed out that he admits in the text that the ciliated cells at least partially travel inwards. On p. 299 after pointing out that "all the columnar cells cannot be transformed into flat cells," he says that the appearances suggest "that the ectoderm [*i.e.*, ciliated] cells are migrating at this point into the interior of the larva," and again on p. 319 he admits that "some of the ectoderm cells of the larva migrate into the interior during the metamorphosis". On p. 375 he makes the confession: "My observations on

the actual transformations of the ciliated cells . . . into the flattened epidermis . . . are . . . meagre" (yes, indeed!), and again admits on the same page "the immigration into the interior of a part of the ciliated cells". For all these reasons it seems to me not only justifiable but even necessary to regard Wilson as a supporter, in spite of himself, of the view that the layers become reversed during the metamorphosis. Wilson's memoir seems, in fact, to have been born out of due season, so to speak; an anachronism, as Maas has well termed it. Commenced, and apparently for the most part written, at a time when the inversion of the layers was not for a moment suspected, when Metschnikoff's almost prophetic statements (1874) had been forgotten apparently even by their author, Wilson's work came forth in an epoch in which the stand-point which it represented had already been clearly shown to be impossible, and the views it put forth were antiquated before they were published.

Nöldeke (1894) on the other hand, sees the facts of sponge development in a very different light. In the larva of *Spongilla* he has described in a most convincing manner the way in which the ciliated layer becomes broken up and carried into the interior after fixation. But with regard to the ultimate fate of these ciliated cells, Nöldeke's views are original and peculiar. He believes with Delage that the amœboid cells of the inner mass capture the ciliated cells and engulf them, in a manner analogous to phagocytosis (see SCIENCE PROGRESS, May, 1894). But whereas Delage believes that the cells so captured are set free again to form the chambers, Nöldeke is of opinion that they are completely absorbed and digested by the phagocytic amœboid cells. In other words he agrees with Goette, whose views have been quoted above, to the extent of believing the external ciliated layer of the larva to be lost, though not thrown off, during the metamorphosis, so that the whole sponge is built up from the inner mass alone. In this mass epidermic cells, amœboid cells and formative cells (Bildungszellen) are to be distinguished. The chambers are stated to arise from the latter, either by division up of a single cell, or by a coming together of cells from different

parts. Nöldeke, like Goette bases his theory of the loss of of a whole germ layer in sponges entirely on observations upon the development of *Spongilla*. How cautious we should be, however, in drawing any far-reaching conclusions from this apparently highly modified type is obvious from the fact alone that its development has been investigated by Ganin, Goette, Maas, Delage and and Nöldeke, and that the observations of all these authors contradict each other upon even most essential points. Indeed, there is hardly any statement, even of detail, which is borne out by the testimony of a majority of the witnesses. I refrain on that account from a detailed criticism of Nöldeke's descriptions and figures, though a close examination might perhaps yield, as in the case of Wilson, results not quite in harmony with the author's conclusions. I will only say that while on the one hand the author's observations as to the immigration of the ciliated cells at the metamorphosis are most valuable and highly to be welcomed, on the other hand the theory of the complete absorption of these cells requires far more convincing proof, both for *Spongilla* and in the case of other types, before it can be entertained.

Goette, whom Nöldeke follows, attempted to give his theory of the loss of the "ectoderm" in sponge larvæ a wider basis of fact by interpreting in this sense the observations of Metschnikoff upon Calcareous Sponges—*Sycandra* and *Ascetta* (*Clathrina*). As regards *Sycandra*, few will, I think, deny that Schulze's well-known investigations render such an interpretation impossible. This conclusion is further borne out by my own observations on the amphiblastula of *Leucosolenia*, where I was able to trace the origin of the collar cells from the ciliated cells of the larva. In the case of other Ascons also I must give a most decided denial to the supposition that the ciliated cell layer is lost in development.

It may be said, therefore, that the embryological investigations upon sponges published since my review in the pages of SCIENCE PROGRESS, to which reference has already been made, tend on the whole to strengthen greatly views there advocated; namely, that a complete reversion of the layers takes place in the metamorphosis, whereby the ciliated

external layer of the larva becomes the internally placed collared epithelium of the adult, while from the inner mass of the larva arise the remaining tissues of the sponge body. There still remain two important cases where statements to the opposite effect remain on record uncontradicted, namely, the cases of *Halisarca* and *Plakina*. In view, however, of the great similarity of their larvæ to those of the lower Ascons it is difficult to believe their development to be of so fundamentally different a type as the recorded observations would force one to suppose. In the present condition of our knowledge it seems to me, that wherever statements exist to the effect that the inner and outer layers of the larva pass respectively into the inner and outer layers of the adult, we are justified in regarding such statements as false until they are proved to be true, instead of believing them to be true until they are proved to be false.

In order to complete and conclude our review of the main features of sponge embryology, there remains one small but important point for discussion; namely, Do the collar cells so characteristic of the adult ever occur in the larva? The point is one which has been thought to be of considerable importance as bearing upon the question of the affinities of sponges with Choanoflagellata. Kent, who as we know was a firm believer in a close relationship between the two groups, described collar cells with large and distinct collars as occurring in numerous larvæ, and tried to prove that the sponge larva was nothing more than a "colonial aggregation of typical collared zooids" (1881, p. 183). He also quoted Barrois (1876, pl. xv., fig. 29) as having figured similar collar cells in sponge larvæ.

Schulze (1885) on the other hand set himself to disprove Kent's statements, while arguing (p. 189) that on the theory of a descent of sponges from Choanoflagellata it might be expected that collar cells would make their appearance in that phase of sponge development which corresponds to a Protozoan colony in phylogeny, namely, in the blastula stage. Schulze, however, searched in vain for collars to the ciliated cells of *Sycandra*, and declares himself convinced (p. 182) that Kent's figures of "swarm-

gemmules" represent simply portions of the collar cell layer set free. Few, I think, will dispute the correctness of this interpretation, and it is easy to confirm Schulze's statement that such appearances can be readily obtained by teazing up living sponges, when also true larvæ may be set free with plates of collared epithelium sticking to the posterior pole, as figured by Kent (pl. ix., fig. 26). Schulze further interprets the hyaline and refractile margin figured by Barrois in the ciliated cells of *Oscarella lobularis*, not as a collar, but as the solid non-granulated terminal portion of the cell.

Shortly after Schulze's very thorough refutation of Kent's statements, Heider (1886), in his studies upon the development of *Oscarella lobularis* resuscitated the collars already described in the ciliated cells of the larva of this form. He found that each flagellum arose from a cup-shaped depression of the hyaline margin of the cell, and regarded this as the rudiment of a collar. The appearances figured by Barrois as the "collier des cellules" were explained as the rudimentary collar together with the hyaline cell margin. But he considered the occurrence of collar cells in sponge blastulæ as of no phyletic significance.

Heider's description of the structure of the ciliated cells of the *Oscarella* is very clear and convincing, but at the same time it is an open question whether such a shallow depression can really be regarded as a true collar. In any case I am unable to agree with him that the occurrence of collar cells in the blastula would be of no phyletic significance. At the same time I find myself unable to endorse Schulze's opinion, that the theory of descent from the Choanoflagellata should have as a necessary consequence the occurrence of choanocytes in the larva. For though the blastula no doubt represents a protozoan colony in phylogeny, it only represents it morphologically, and not physiologically; that is to say, the cells are not functionally active, except as regards locomotion, since they do not take in food, or at least have never been observed to do so. The collar, however, is always a sign of functional, and especially nutritive activity, most developed when the sponge is most expanded, and always to be found more

or less retracted, often completely so, when the sponge is contracted and closed up. Hence, for my part, I should not expect to find the ciliated cells of the larva provided with collars, even if it were quite certain that the theory of choanoflagellate descent were the true one. But on the theory of the continuity of the ciliated cells, which we have already discussed, the ciliated cells of the larva pass directly into the collar cells of the adult and develop collars after the metamorphosis, when the sponge begins to feed and grow. Hence it follows that the ciliated cells of the larva do possess the power of developing collars, and might be regarded as potential collar cells, in which the function of nutrition is temporarily in abeyance, and as a result the collars are not protruded.

From the foregoing review of sponge characteristics we may pick out four points of primary importance in the discussion of their affinities :—

(1) The unfailing possession of collar cells, and their great resemblance to Choanoflagellata. This, as we have seen, is the feature which has been the mainstay of those who advocate the relationship of sponges to Choanoflagellata or their descent from them, while those who advocate a contrary view are obliged to minimise the resemblances, or declare them due to analogous adaptation.

(2) The reproduction by ova and spermatozoa. This, on the other hand, is a feature which has furnished support to those who regard sponges as Metazoa of some sort or other. In view, however, of the many analogous sexual processes known to occur amongst Protozoa and in plants, it is perhaps not safe to lay too great stress upon this point, especially as the details of the process seem to be of a type rather more primitive than in other Metazoa.

(3) The formation of two germ layers by processes not specially characteristic of sponges, and the possession of a larva very similar to the cœlenterate planula. This is certainly the strongest argument for the Metazoan affinities of sponges, and has always been much employed by the supporters of this view, especially by the cœlenterists. We have already quoted many of the arguments based on this

point; they were well summed up by Schulze (1885, p. 191) when he asserted "that the difference between the free swimming ciliated larvæ of sponges on the one hand, and of Cnidaria on the other, is not more considerable than the difference among sponge larvæ themselves".

(4) The reversion of the layers at metamorphosis. This fact, now sufficiently well established, is quite subversive of the cœlenterate theory. It is only necessary to read the arguments of the cœlenterists to see at once how completely it undermines their position. The cœlenterate theory assumes as the type or "Grundform" of sponges a hollow sac-like or vase-like organism, with the body wall composed of two layers, ectoderm and endoderm, and derived from an embryo composed of the same two layers similarly orientated. If, however, we make our comparison start from the adult forms, then the larvæ of sponges are quite anomalous, in that they possess an *ectoderm* derived from the *macromeres*, and often completely surrounded by the endoderm. If, on the other hand, we lay stress on the resemblances between the larvæ any comparison of the adult sponge to a cœlenterate is out of the question.

When, however, we try to decide by means of this point whether sponges are or are not Metazoa, we do not get much help, since in either case the interpretation of the ancestral history presents much difficulty. If the larva, say of a simple Ascon, be regarded as strictly homologous with the very similar larva of a hydroid, it is very difficult to understand why in the one case the component layers should be reversed at fixation and in the other case not. If on the other hand we regard the Ascon parenchymula larva as a repetition in development of an ancestral stage similar to *Proterospongia*, a free-swimming volvox-like colony of Choanoflagellata in which certain zooids were continually migrating into the interior, it is by no means easy to form a clear idea of the steps by which such a form came to reverse its layers and place its collared cells in the interior. Hence the metamorphosis of the sponge larva cannot be regarded as affording conclusive arguments in favour of either the metazoan or the choanoflagellate affinities of sponges. In so far, however, as it indicates

the ciliated cells of the larva to be potentially collared cells, as pointed out above, the reversion of the layers is slightly in favour of the choanoflagellate theory.

It is very evident that we have at present but two theories to choose between; either to regard sponges, with Bütschli, Sollas, and Delage, as descended from choanoflagellate ancestors independently of the Metazoa; or to regard them with Maas and, apparently Balfour, as true Metazoa composed of the two primary germ layers, ectoderm and endoderm, which have become reversed in position in the adults. The choice between these two theories will depend upon which of two assumptions we find most difficult. If sponges are Metazoa, the collar cell, occurring in no other Metazoa, must have been independently acquired. If sponges are descended from Choanoflagellata, then the sexual reproduction, the segmentation of the ovum, and the formation of the two germ-layers, must be processes analogous, and not homologous, with the similar processes in Metazoa. For my part I must confess that the second assumption seems to me at present the hardest to swallow. The theory of the metazoan nature of sponges offers in the present state of our knowledge fewer difficulties than the theory of independent descent from the Choanoflagellata. Whether or not a closer acquaintance with the structure and development of sponges will confirm this view remains to be seen. How cautious we should be in pinning our faith to either one of these positive views is sufficiently shown by the history and present position of the cœlenterate theory.

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THE DISEASES OF THE SUGAR-CANE.

PART II.

THE first part of the present essay[1] was devoted to a consideration of the general character and prevalence of diseases in the sugar-cane. An attempt was made to determine whether this tropical plant, cultivated for thousands of years, is in reality more subject to the attacks of parasites in the present day than in past times. And the conclusion arrived at was that, although the diseases were in many cases severe and widespread, there was no good ground for supposing that the cultivation as a whole was threatened from this cause.

It is none the less evident that, in the economic crisis through which all sugar-growing countries are at the present moment passing, disease phenomena cannot be neglected. It may well be that estates, just able to hold their own against the severe European competition, would have the scale turned against them by any unhealthiness in their canes. The study of the pathology of the cane-fields must therefore go hand in hand with the improvement of machinery and reduction of expenses now acknowledged to be absolutely necessary.

In the present article it is proposed to discuss the way in which this problem has been attacked in the Tropics. Amid the general apathy of the planters, good hard work has been done by the few who foresaw the threatening danger; and the scientific men in our own, as well as in other countries, have spared neither time nor labour in their endeavour to improve the general agricultural condition of the cane plants. Attention was, in the first instance, devoted almost entirely to animal parasites; and the remedies suggested were drastic, and pointed directly at their extermination. It was proved later that fungi of various kinds were attacking the canes as well; and for a

[1] Barber (1).

time attention was exclusively paid to these vegetable parasites. Lotions and sprays, destructive manures, digging up and burning were the order of the day. It is now being gradually recognised that success by these *direct attacks* is beyond the powers of man. *Indirect methods*, having in view the strengthening of the cane's constitution, are in vogue, on the principle of "less poison and more circumvention". The adaptation of the different varieties of the sugar-cane to soil and climate are more carefully weighed: fresh varieties are introduced and attempts are being made to obtain new and improved strains by means of vegetative and sexual selection.

2. The literature dealing with the *direct remedies* is immense and it will serve no useful purpose to attempt to summarise it, especially as many of the earlier suggestions were made without a knowledge of the true cause of the disease.

In the days when plagues were attributed to the malign influence of supernatural powers, the cure consisted in religious assemblies and votive offerings. We thus find it recorded by Oviedo and Herréra that the whole island of Hispaniola was subject in the early days of cane cultivation to the attacks of a species of ant, which in 1518 overran the island, devouring all vegetation, causing famine to the inhabitants, and nearly depopulating the island. "In order to get rid of these scourges, great processions and vows were made in honour of St. Saturnin; the day of the saint was celebrated with great solemnities, and *the ants disappeared afterwards gradually.*"[1]

The "sugar-ants," *Formica omnivora*, which appeared in immense quantities in the cane-fields of Barbados and other islands in 1760 were, on the contrary, attacked by the planters with the greatest ferocity—the latter not appearing to have any superstitions in the matter. Poison and fire were freely employed. Corrosive sublimate was found to be most effective, the ants becoming insane and pulling one another to pieces. Burning charcoal was quickly extinguished by the immense numbers which threw themselves

[1] Schomburgk.

upon it. Pits were accordingly dug at intervals in the cane-fields, and a fire made in each. The flames were quickly smothered, the place of each being marked by a heap of dead ants the size of a mole-hill. These direct attacks appear to have been entirely unsuccessful, and the ants only disappeared after a hurricane in 1780.[1]

A distinct advance is to be noted in the advice given by S. Martin Senr., about the same time, with regard to the "blast," probably an aphis, attacking the canes in Antigua. He recommended the use of "wooling raggs dipped in soap-suds after having been used in washing cloaths"—an early reference to the spraying of plants so widely adopted at the present day.[2]

3. The remedies applied during more recent years have usually borne directly upon the natural habits of the past. A careful study has now been made of the life-history of many of the parasites, in order to select the stage in which the application of insecticides and germicides would be most successful. This varies considerably in different cases. The grub appears to be the point of attack in the moth-borer, the freshly hatched young in the scale-insect, the egg-cases in locusts, and the adult beetle in the Java pest, *Apogonia destructor*. Although the life-history of the latter has not apparently been determined beyond dispute, it has been very carefully studied by Kobus,[3] Zehntner,[4] and other zoologists, and may serve us as an example.

There are usually two main flights of mature beetles, one in November and one in March. The larvæ attack the cane roots between these dates, the injury first becoming noticeable in January. The larger, November, flight is determined by and closely follows the west monsoon, which also brings the first rains. Beetles collected during the last days of October have very immature generative organs and no food in their alimentary canals. They feed at night upon various leguminous plants (*Sesbania*, *Arachis*, *Soja*, *Tamarindus*) and push themselves under the loose earth at sunrise. Specimens dissected in the early days of November frequently have well-filled digestive organs, and, later in

[1] Schomburgk. [2] Martin [3] Kobus (1). [4] Zehntner.

the month, the generative organs mature, and copulating specimens may be captured. The eggs are laid in moist earth and hatch in six to eight days. The larvæ feed on the cane roots for a couple of months or more, as many as sixty having been found upon one plant. The pupal stage lasts for a week, and the beetles, emerging, cause the March flight. These, on dissection, are seen to have empty alimentary canals, and extremely rudimentary generative organs. After feeding for a certain time, the beetles now cease to leave the ground at night, are less abundant as the east monsoon (April) brings the drier weather, and later disappear till the succeeding west monsoon, with its rains, causes a sudden resurrection. These observations point to a yearly brood of young in December. The means adopted is, therefore, to catch the beetles when they appear after the rains, and before they have laid their eggs.[1] Enormous numbers are obtained by shaking the leguminous plants near cane-fields over sheets at night, and large quantities are also obtained by loosening the earth under such plants during the day.[2]

The collection of moth-borer grubs is carried on in the young cane-fields. Plants attacked are readily noted at that stage and destroyed with their contained grubs. Later on, when the canes become large, it is difficult to penetrate the fields, and, furthermore, it is difficult to obtain a cane which is not attacked, so that the destruction of infected canes when well grown would practically mean the reaping of the whole crop.[3]

This destruction of moth-borer grubs and mature Wåwålan beetles before they lay their eggs may be taken as typical of this class of carefully thought out remedies. The indiscriminate liming, trashing, treatment with insecticides and burning have less to be said for them. Owing to the nature of the growth of the sugar-cane, its parasites are peculiarly inaccessible to ordinary methods of treatment. The burning of fields is frequently the only means of reaching them, and this is a step with very grave consequences in the Tropics, because of the destruction

[1] Zehntner. [2] Barber (1), p. 301. [3] Watts.

thereby of the carefully fostered moisture-yielding humus. Consequently this method is not recommended or adopted excepting in extreme cases.[1]

4. A more promising field of activity seems to be opened up in the encouragement of the enemies of parasites. We know, for instance, that the moth-borer itself has many minute enemies which feed upon it and tend to keep it in check.[2] Is it possible so to increase these latter as to render the very existence of the moth-borer doubtful?

But success in this direction is accompanied by many difficulties, and needs comprehensive knowledge of the interdependence of the various forms of animal and vegetable life.

One of the most interesting examples of this class of remedies is the recent introduction of the *Mongoose* from India to the West Indies, for the purpose of ridding the fields of the swarms of rats which destroyed great quantities of ripe canes. The experiment, suggested so long ago as 1814 by Lunan,[3] may be regarded as having been successful in the main; although its most ardent supporters cannot claim that the success has been unqualified. The rats have, it is true, disappeared from the fields; but the mongoose, having enormously increased in numbers, has turned its attention elsewhere for food. Not only are the poultry-yards boldly attacked, but game and all sorts of ground birds and lizards have almost disappeared. Urgent appeals have now been addressed to the Governments of various islands to take measures to destroy the mongoose. Its introduction has disturbed the balance of nature. The native insect-destroyers have been decimated, and many see in this one rash step the cause of all the ills of the cane-fields! The introduction of a few pairs of mongoose has produced results neither dreamt of nor desired, but probably legislative action will be futile. The animals have apparently reached their limits as regards numbers, and the judicious introduction of tree-nesting insectivorous birds might do much towards recovering an equilibrium.[4]

An interesting attempt is recorded to inoculate the rats

[1] Harrison (1). [2] Barber (1), p. 308. [3] Lunan. [4] Mongoose.

of Mauritius with a mouse disease—without apparent success.[1]

Nothing appears to be done in the way of encouraging the various enemies of the moth-borer. The small egg-destroying *Hymenoptera* may be left to their good work, but no means suggests itself of increasing their powers. An attempt has been made by Watts to inoculate the moth-borer caterpillars in Antigua with the spores of *Isaria Barberi* and also of *Botrytis tenella* received from Giard in Paris.[2] Similar attempts have been made with Java moth-borers, and by Kobus with the beetle Wâwâlan.[3] These have not thus far proved successful. It seems, after all, as if little, if anything, can be accomplished along this line of attack. The mutual relations of the various members living in any one district must be much more clearly traced: the laws by which certain forms suddenly increase out of all proportion and without apparent reason during a single season: the conditions which lead to their almost total destruction by parasites—all these must be better understood before we can hope to sow diseases and call epidemics into being, and by this means protect our cultivated plants from their parasites.

5. A useful defensive measure is sometimes found in the careful demarcation of disease areas and the observance of strict quarantine. The introduction of plants from one region to another is rendered dangerous by the remarkable fact that the diseases which attack cultivated plants in one country are frequently harmless in others and *vice versa*,—that the virulence of a disease in any one plant varies with the locality as well as at different times in the same locality. Great care is therefore necessary lest the importation of new varieties into any district should lead to the introduction of new diseases. A striking warning is met with in the history of the replacement of European vines by American ones. The leaves of the latter were found to be more resistant to the vine mildew (*Oïdium Tuckeri*), and were consequently introduced into Europe.[4] The appearance of these American vines in Europe was followed, in

[1] Boname. [2] Giard; Wakker. [3] Kobus (2), (3); Wakker. [4] Esser.

1863, by *Phylloxera vastatrix*, a coccid which was known to be present on the roots of American vines. In Europe, however, its attacks on the roots of the vine were much more virulent. It is estimated to have cost France alone many times as much as the war indemnity paid to Germany. In 1877, the continued importation of American vines brought over *Peronospora viticola*, a parasite even more deadly than the *Phylloxera*. In each of these cases a parasite was thrust into the midst of a cultivation utterly unprepared by natural selection to withstand its attacks—a result which would certainly have been avoided with careful legislation on the free distribution of cultivated vines.

The Mallow disease, *Puccinia Malvacearum*, introduced into Europe from Chili, affords another example of the amazing damage which a mild parasite may cause if introduced into a new country.[1] For some years there did not probably exist an exposed Malvaceous plant in Europe which was not severely attacked. In certain localities, it will be remembered, hollyhocks could not be grown because they were destroyed by *Puccinia* before reaching the flowering stage.

It is quite certain that many cane diseases have been propagated in this way. As will be seen later, it is an established custom in many parts of the world to send cane plants from one district to another, since by this means a better growth is obtained. Cane plants thus introduced from Ceylon into Mauritius are supposed to have caused the severe epidemic of borer grubs already noted.[2] These facts, and others of a similar nature, have led to a carefully marked out system of plant distribution in Java. It was found that plants brought from the mountains and planted in the plains were much less liable to sereh. It was further noted that certain districts were comparatively free from sereh. These parts of the island were marked off and placed under strict protection. No cane plants whatsoever were allowed to be introduced into the free regions, whereas plants were freely supplied from them to the plains. Thus we read successively of three more or less sereh-free regions,

[1] Cooke. [2] Bojer.

Malang, Tangerang and Preanger.[1] Severe penalties have been enforced against planters disregarding the quarantine regulations, and a constant supply of sereh-free plants has thus been obtained to stock the fields and nurseries of infected districts.

6. It is worth while noting, however, that direct attacks upon a parasite are usually futile. It is difficult to point to a single instance in which a widely distributed pest has been stamped out by these means, and it is not usual to pay much attention to a disease until it is widespread. And this has led the students of plant pathology to turn their attention in another direction. Is it not possible so to strengthen the plant as to render the parasitic attacks harmless?

This may be attempted in two ways; by the perfect adaptation of a plant to its surrounding conditions of growth, and by the encouragement in a plant of some peculiarity which is distasteful to the parasite. In the former case careful attention must be devoted to external surroundings so as to produce healthy, vigorous growth; in the latter it is necessary to produce a new variety. In nature both of these principles are unceasingly at work; among cultivated plants it is needful to see that they are not absent.

7. The choice of climate, class of soil, mode and efficiency of cultivation and manuring require constantly to be considered.

The cultivation of any plant in a climate unsuited to it produces a weak form liable to disease. The value of the larch as a timber tree has led to its being planted far beyond its natural limits, with the resulting appearance of a dangerous disease—the larch canker. It would be idle to ignore the fact that different varieties of the sugar-cane vary much as to requirements of soil and moisture. While some, such as the *Bourbon*, are best grown in clayey soils with a considerable amount of rain, others, such as the *Transparent* kinds prefer a light volcanic well-drained soil.

The result of growing the much-valued *Bourbon* in

[1] Kobus (4), (5). Werot (1).

unsuitable places was well exemplified in the recent outbreak of shot-borer (*Xyleborus perforans*) and rind-fungus (*Trichosphaeria Sacchari*) in St. Kitt's cane-fields. The island was roughly divided by an imaginary line across the mountains into the region under *Bourbon* and that under *Caledonian Queen* (a transparent cane). The former cane found many admirers, although clay is unknown in the island (except a few acres above the limits of cane cultivation), and the soil consists everywhere of deep layers of volcanic ash. A careful examination of all the estates in the island showed the diseased area was roughly that of the *Bourbon* cane, the estates under *Caledonian Queen* being practically free from injury.[1]

8. The general character of the cultivation is of equally obvious importance. There is no question that the cultivation in most sugar-growing countries has vastly improved in the last quarter of a century; and very possibly this is the reason why many diseases, formerly abundant, are now of little account.[2] The epidemic of *rust* in Queensland has been referred to careless cultivation, following upon too great success in the first opening up of virgin soil.[3] Two root parasites, *Alectra brasiliensis*[4] in Dominica and *Striga euphrasioides*[5] in the Central Provinces of India, both belonging to the *Scrophulariaceæ*, are found to thrive in waste, neglected cane-pieces, but disappear when the land is kept in order. The *gumming* of Pernambuco has been traced by some as primarily due to bad drainage and condition of soil.[6] The most fruitful cause of cane-disease in India is stated to be the carelessness following years of great prosperity.[7]

On the other hand, good cultivation is not always a remedy for disease. Certain epidemics among the canes are due to other causes than the mere supply of proper nutriment to the plant. The utmost care in cultivation has had small effect for instance upon the *gumming* in Mauritius, the *sereh* in Java or the *rind-fungus* in the West Indies.

[1] Barber (2). [2] Barber (1) p. 311. [3] Barber (3). [4] Barber (4).
[5] Watt. [6] *Sugar-Cane*, 1894, xxvi., 377. [7] Watt.

9. The question of manuring is a difficult one. Many have put down the increase of disease in the cane-fields to this cause. A lack of adjustment between stimulating and feeding manures will certainly lead to crops of small resisting powers; and little trouble has been taken in the past to determine the needs of the plant in different soils. Scientific manuring will vary with almost every field, depending not only on the chemical composition of the soil, but also on its physical condition. In the great majority of cases, general cane manures have been used without special study of the soil, resulting in waste and, possibly, injury to the plants. But while artificial manuring has probably been harmful in certain cases, the principle is sound enough; and those have far more reason on their side who trace the prevalence of disease to the exhausted condition of the soil on the worn-out estates where manuring has been neglected. The careful comparison of the effect of different combinations of manures upon certain selected canes has been a subject of special study in the various *sugar experimental stations*.[1] A mass of facts has thus been accumulated which should place every planter in a position to test the requirements of his own fields. No praise is too high for the patient manner in which the various Government analysts have pursued these studies, frequently amid the ill-concealed hostility of the planting body.

It is well known that excessive nitrogenous manuring renders *corn* more liable to *rust*;[2] and a similar observation has been made regarding the sugar-cane. In some carefully conducted experiments on a Demerara sugar-estate to determine whether any relation existed between disease and manure, Harrison has demonstrated that the amount of disease was largely proportional to the nitrogen in the manure.[3]

10. A good deal of study has been devoted to determining the chemical constitution of the cane at different periods of its growth,[4] as well as the comparative composition of healthy and diseased canes, without, however, having at present yielded much result of economic import-

[1] Reports. [2] Berlese. [3] Harrison (2). [4] Went (2); Sagot *et* Raoul.

ance. A careful analysis of diseased canes has been made in various countries, one frequent result being a deficiency of silica in the ash. Stutzer found that the plants suffering from sereh had deficient silica and excess of potash, and suggested that, among other remedies, a rational system of manuring might be applied to sereh.[1] Francis, in canes attacked by rust in Trinidad, found 36·01 per cent. of silica in the ash instead of 45·84 per cent.; and Liversedge, examining Queensland canes also suffering from rust, found the deficiency in silica much greater, the diseased canes containing only 25 per cent. or 30 per cent. of the normal quantity.[2] It does not appear how this state of things is to be altered.

The idea has been advanced in certain directions of altering the cell-sap by the addition of special substances, such as copper sulphate to the soil,[3] and thus rendering a plant more capable of resisting the attacks of a parasitic fungus. But sufficient stress does not seem to have been laid on the selective power of the plant itself. Changes are probably constantly taking place in Nature by which a plant renders its juices less palatable or nutritious to its parasite, but it is doubtful whether any system of manuring will ever succeed in thus directly altering the cell-sap.

11. It is quite certain that the cells of plants are more or less resistant to disease according to their age. Young cells by their greater vitality are able to resist the action of the ferment emitted by an attacking fungus. The older cells, with their stores of reserve materials and less active protoplasm, on the other hand, are frequently guarded by the presence of special substances, *e.g.*, tannin in many cells, ethereal oils, resins, etc. The tendency of cultivation is, however, to eliminate these latter substances; and this will possibly account for the time of appearance of certain diseases.

The rind-fungus, *Trichosphaeria Sacchari*, may be present in the young tissues, but it is one of the characters of the disease that it becomes first evident by the discoloration of the mature joints in the middle of the cane, where

[1] Stutzer. [2] D'Albuquerque, see also Boname. [3] Berlese.

the protoplasmic lining of the cells is very thin and the large sap cavity abundantly stored with sugar. The fact that the joints first showing signs of disease are not the lowest and oldest may be explained by the greater exposure of the higher ones (12th or 13th, according to observations of the author), which are consequently more freely tunnelled by the moth-borer, and thus bared for the fungus spores. There is a small step between such cells and those actually dead, and in New South Wales the rind-fungus appears principally to attack canes near the point of death.[1]

The apparent periodicity observed in sereh seems to be due to a different cause. The disease makes its appearance shortly after the rains, because the stricken canes alone refuse to shoot up. The rains again bring about the appearance of the swarms of wåwålan in Java, awakening them from their summer sleep. It has frequently been noticed that plant canes and ratoons (second growths from the cut plants, the roots being left in the ground) are differently attacked by disease. The "plants" seem to be more severely affected by gumming and rind-fungus, a fact which may depend on the older and stronger root system of ratoons. On the other hand, in sereh the disease appears to increase steadily all through the life of the plant, being much more severe among ratoons. As a result of this, while ratooning is to be encouraged in places attacked by rind-fungus, it has practically disappeared from Java.

12. One of the most interesting features in the study of cane diseases is the apparent immunity of certain varieties. Taken broadly, the "soft" canes are the ones most liable to disease, while the "hard" canes are more or less resistant. It is not likely that the juiciness of the stem or the hardness of the "rind" is of itself a direct factor in the matter, but it is fair to infer that these characters are among a series of correlated ones which render the plant a more or less easy prey, just as we are told white chickens are more liable to gapes and white verbenas to mildew.[2] The *Cheribon* cane is especially subject to

[1] Cobb. [2] Darwin.

sereh in Java; in Mauritius the *Bamboo* cane is most liable to gumming; while in the West Indies it is the much esteemed *Bourbon* which is principally threatened by the rind-fungus. In each case the predominant cane is most attacked. Each of these three is a "soft" cane. What are the characteristics of such a cane? Large, free-growing, juicy, of great saccharine content, and readily torn by the teeth.

In India the *paunda* or native forms are much the hardiest; in Java the seedling canes more nearly approaching the *Glagah* or wild indigenous kinds are free from disease. From this it is easily gathered that the less hardy canes are the outcome of the most careful human selection. Canes left more to themselves and the action of natural selection are invariably better able to resist disease. An interesting example of this is met with in the canes grown in India—probably near to, if not itself, the original habitat of the species. The forms cultivated may be roughly divided into two classes—those used in the production of sugar and those eaten as a fruit. The former are small, hard, not very juicy, and are left more or less to themselves at a distance from the houses. The latter are thick, juicy, with a thin rind; they are planted carefully near the houses, and treated to a garden cultivation. The human selection by which these "soft" varieties have been produced has been one-sided; it has to a great extent neglected liability to disease. Consequently these canes are severely attacked the moment they are left to themselves, and in the field are utterly unable to compete in hardiness with commoner kinds.[1]

This agrees very well with the remark that liability to disease results from an accumulation of certain of a plant's many characters, and that there are all stages between healthy and diseased plants.[2]

13. Attention has already been drawn to the fact that canes are found to be of stronger growth if the plants are occasionally brought from a distance, on the principle that plants, as well as animals, are all the better for an occasional

[1] Watt. [2] Sorauer.

change of climate and food. This has been a custom from time immemorial among the cane growers of India, and has been extensively adopted in most sugar-growing countries.

It is also a firmly established belief that the long-continued planting of any variety in the same locality is certain to engender a diseased condition. Many interesting and striking examples of this might be quoted. In 1840 the Bourbon cane was introduced to Bogra, one of the chief sugar-growing parts of Bengal. For eighteen years it succeeded remarkably well, and practically displaced the older native varieties, and those who had adopted it became rapidly rich. In 1857-1858 a disease suddenly appeared which left the canes rotting on the fields, and in the succeeding year or two the Bourbon cane disappeared from cultivation.[1]

Cases of this kind—and many others might be quoted—may be explained in the following way. A variety introduced into a new country is at once placed among a new set of parasites. Sometimes these are able immediately to assert themselves, rendering acclimatisation difficult. Others require a certain number of years before they can adapt themselves to the protoplasm and cell-sap of the new variety, after which they rapidly destroy it, unless it has a similar or greater adaptive power. This seems to account for the sudden destruction of the Bourbon cane in the Central Provinces of India. In the same way it was several years before the *Peronospora viticola*, already referred to as coming from America, was able to overcome the natural resistance of European vines. Once able to do so, it became an active and dangerous parasite.

14. We may conclude then that continued planting in the same soil need not cause a deterioration in the cane, especially as there are many districts where the Bourbon has been grown for years without an appreciable increase of disease (as in Demerara). It has been urged by many that the exclusive vegetative reproduction of the sugar-cane, without the chance of an occasional cross, is bringing about a gradual decline of vigour. This may

[1] Watt.

perhaps be the case, but it does not explain the hardiness of the resistant varieties which have been propagated in a similar manner. The nearest allies of the sugar-cane among wild forms appear also to be apogamous,[1] so that vegetative reproduction is probably a natural mode of increase. There seems, in fact, to be no more reason for deterioration in the sugar-cane from this cause than there is in oranges, vines, pine-apples, and other fruits propagated in this way.[2]

As far as can be gathered from the past history of these "soft" canes, one of their characters has *always* been that they are especially liable to disease. The first references to the Bourbon cane in Jamaica, India, Antigua, Queensland and Pernambuco seem, indeed, to unite its great value as a sugar producer with a certain tenderness. There seems then to be no valid reason to assume that the canes most prized in cultivation are deteriorating. They are the best results of the careful human selection of centuries. Sufficient care has not been exercised to bring out disease-resisting properties, as well as those of sugar production; but this is a point now held to be of first importance in all sugar-growing countries.

15. The search after new varieties of the sugar-cane is by no means a new one. Selection has been at work for thousands of years, and, thanks to it, we have at present hundreds of varieties, many of them capable of producing excellent results.

Within recent years attempts have been made to determine the limits of asexual or vegetative selection. A series of laborious experiments have been conducted by Edson in Louisiana with the object of finding out whether, by planting the richer canes of a field, a richer variety may be built up.[3]

The results thus far are in favour of such a method in the United States. It has, however, been urged in Java, and elsewhere in the Tropics, that the richer canes of these localities are not capable of improvement to the same extent as the poorer Louisiana canes—the sugar content of the

[1] Sagot *et* Raoul. [2] Möbius, see also Went (3). [3] Edson.

Cheribon in Java, for instance, being assumed to be near perfection.[1]

Attempts at creating a disease-proof variety of "soft" cane are more to the point. This has engaged much attention in Java, and a certain amount of success has already been attained. The method suggested is the following: Select plants which were living as long as possible before the first general appearance of sereh. The chances are that such plants have a more or less resistant character. Form a new plantation from the best of these, using only perfectly sound canes for planting. Constantly weed out those attacked by sereh.[2]

16. The principal objection to this method is its slowness. A more rapid, but less reliable, means of obtaining a new variety is by *bud-variation.* It occasionally happens that a plant produces a bud quite different from the rest in foliage and other characters. If the shoot thus produced can be used for propagation, a new variety will probably be obtained, because its peculiarities will remain fixed as long as the vegetative method is adhered to. If, however, the variety thus obtained is allowed to seed, it at once loses its assumed characters, and tends to revert to the parent type. It is exceedingly rare that such a variation is detected in the sugar-cane, and the probability of its occurring in an entirely useless direction practically removes bud-variation from available methods.

Another possible way of obtaining new varieties asexually is by what are known as *graft-hybrids.* This subject appears, however, to be rather obscure, and the cases in which success is claimed do not always bear very close examination. It occasionally happens that in grafting a shoot arises from the point of union of stock and scion, presumably by fusion of the parent cambiums, and unites the characters of the parents. It will be seen at once that graft-hybrids must be of rare occurrence, when we consider that the operation of grafting is principally performed when it is desired to perpetuate the characters of the scion unaltered. There seem to be authentic cases of varieties arising in this

[1] See *Sugar-Cane*, 1894, xxvi., 73 and 271. [2] Went (4).

way. Attention is drawn to it in this place because of recurring statements as to the value of this method in certain sugar-growing countries. In the absence of the means of determining their truth, it is useful to inquire how far grafting will succeed in Monocotyledons, where there is no cambium, and especially whether the sugar-cane is amenable to this treatment.[1]

17. The main lines along which selection must be followed are, however, by the production of seedlings. It is a noteworthy fact that many varieties of plants, especially cultivated ones, cannot reproduce true from seed. Of ordinary fruit trees, for example, small, sour, and uneatable fruit are borne by 90 per cent. of seedling peaches, 93 per cent. of plums and 97 per cent. of pears and apples.[2] New varieties are therefore certainly and readily obtained by crossing; it is also patent that such varieties are in the great majority of cases useless reversions to an uncultivated or natural condition of the plant.

The variability of the sugar-cane has been amply demonstrated among the collections of spontaneous seedlings as well as those raised by artificial crossing.

For many years the cane was held to be incapable of producing fertile seed. This is the more remarkable because many eminent botanists have paid special attention to the subject both in India and the East and West Indies. In all probability multitudes of seedlings have been produced year by year in favourable localities; but from some cause, perhaps their similarity to grasses, no one succeeded in detecting them.

The arrowing or flowering of the cane is a very well-known feature in tropical scenery, yet in parts of India, where the sugar-cane is grown, the flowering is of very rare occurrence. It is mentioned by Dr. Kobus in his account of his journey to Saharanpur to obtain new varieties for cultivation in Java, that he met with people who had never seen the arrows, and did not know in what part of the plant

[1] Barber (5); see also Darwin, Sorauer, and *Louisiana Planter*, April 17, 1897.

[2] Went and Geerligs.

to look for them. Whether this was at all a common occurrence or not, it is certain that the arrowing of the cane was regarded with superstitious dread. Brahmins have been known to desert a district in which it occurred.[1]

This constant cutting of the canes before the flowering period arrived, and the consequent absence of arrows, has undoubtedly tended to strengthen the belief in the non-fertility of cane-seed. It is now regarded as probable that the sugar-cane has never entirely lost its seeding powers; and there are some who believe that the immense number of varieties which have gradually crept into existence are not bud-varieties but true hybrids.

18. Experiments with seedling canes have now been carried out in every quarter of the globe. Excellent varieties have been reared by crossing; and the nature of seedling canes and the means of obtaining them is well understood. Yet it is barely ten years since the fertility of cane seed became a recognised fact.

The discovery of cane seedlings appears to have been made in the island of Barbados,[2] where we learn that a planter named Parris, in 1858, observed great numbers of seedlings which he carefully reared, but rejected because of the appearance of certain objectionable characters. In spite of the authentic records of this fact, as well as less certain statements regarding the discovery of cane seedlings in Java a couple of years later, the fertility of cane seed was again disputed and these observations almost forgotten.

Natural seminal reproduction seems to be particularly favoured by the climatic conditions in Barbados, whereas in Java the reverse appears to be the case. Soltwedel in the latter island made crossing experiments for years, besides carefully searching the fields, before he succeeded in 1886-87 in proving to his own satisfaction that he could thus produce hybrid canes. In Barbados, on the other hand, a search in the fields by Harrison and Bovell was rewarded by the discovery of many thousands of plants in January, 1888. While the Java results were not made public for several

[1] Watt.

[2] Kobus (6). See also especially *Kew Bulletin*, Oct., 1891.

years, those of Barbados were quickly known all over the world in sugar-growing countries and excited the keenest interest in the subject. In Barbados, Harrison and Bovell, and later, in Demerara, Jenman and Harrison have continued the study of cane seedlings, and to their valuable reports we owe most of our present knowledge on the subject.[1]

The results are, on the whole, satisfactory. As the sugar-cane requires two years for its growth from seed to flowering, seminal selection here is slow work; and those who failed to grasp the subject, and looked for a sudden revolution in the cane-fields, were from the first doomed to disappointment. From the nature of the case, experiments must be conducted on a large scale—a difficult matter with so extremely tender a seedling which grows into so large a plant. Any one reading the Demerara reports will be at once convinced of the proportions of the task set themselves by Harrison and Jenman; and the comparative failure of all but a few attempts elsewhere adds to our sense of the difficulty of the work.[2]

Two main features have constantly to be held in view in these experiments. The variety aimed at must have a sugar yield equal to the best of the old sorts, and it must have a greater power of resisting disease.

The following plant, raised by Prinsen Geerligs in Java, may serve as an example of a hybrid sugar-cane. Of the parents, the *Black Java* cane has infertile pollen and therefore no seedlings of its own; it is much planted because of its rich juice, but it cannot withstand sereh. The *Canne morte* of Australia is vigorous and resists sereh, has a great quantity of sugar and yields heavy crops, but its juice is of inferior sucrose content. The hybrid obtained shows very vigorous growth, with good yield of juice of good quality.[3]

Careful experiments, conducted in this way, are sure ultimately to succeed in producing valuable additions to the varieties of sugar-cane in cultivation, and also to assist in checking the dangerous parasitic diseases to which the better-class canes are liable.

[1] *Reports.* [2] *Reports.* [3] Geerligs.

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RECAPITULATION.

ONE of the commonest errors, or fallacies in science, at any rate in biological science, is hasty generalisation. A statement which is observed to be true in particular cases is frequently stated to be generally true, and the generalisation is widely accepted and commonly taught until some independent critic arises to point out that there are important cases in which it does not hold. The Haeckelian generalisation that individual development is a recapitulation of ancestral development is an example of this. It has been current in various formulæ. Haeckel called it the biogenetic law. Professor Milnes Marshall, I believe, was responsible for its expression in the form that each individual is compelled to climb its own genealogical tree. The pre-Haeckelian statement due to Von Baer was that animals resemble one another more in the earlier stages of their development, and diverge in form as they approach the perfect or adult condition. Mr. Adam Sedgwick has lately attracted considerable attention by a trenchant criticism of the generalisation in all these forms, and has put forward conclusions which are incompatible with it, and which I propose to consider in the course of this article. But it is certain that the doctrine in question has never been supposed by modern working biologists to be literally and universally true. If it were so we should be able to discover the complete evolutionary history of any animal from an examination of its individual development, which is notoriously not the case. In fact it is admitted at the present time by every investigator of evolution that whatever hopes may have been formerly entertained concerning the revelations to be obtained from embryology, we have not obtained, and cannot obtain, from a knowledge of ontogeny or the development of the individual, anything more than occasional indications of phylogenetic history, or the modification of the series of generations. Our great English embryologist, years ago, in his classical text-book,

expressed the truth of the matter when he stated that ancestral stages were liable to be dropped out or omitted in embryonic development, to be hidden or replaced by new characters in larval development. We have long been accustomed to use technical terms to distinguish ontogenetic characters which are probably or evidently recapitulative, from those which have evidently been recently evolved in the larva or embryo: we call the former palingenetic, the latter kainogenetic. What is new therefore in Mr. Sedgwick's paper is not the proposition that ancestral structure is not always recapitulated in the early stages of individual history, or that many embryonic or transitory characters are not ancestral. The main object of the paper is to support a particular explanation of the apparent capriciousness which is observed in the persistence or disappearance of ancestral organs and characters. This explanation is that the retention of an ancestral condition in the series of embryonic changes indicates that this condition was once a larval condition, that is to say, was retained as a necessary adaptive character in a free-living larval stage of the animal, after the new adult character had been evolved. Afterwards the larval stage ceased to be free, the young animal being confined either in an egg-shell or in the maternal uterus until its metamorphosis had been accomplished, when it was hatched or born with a structure more or less exactly similar to that of the adult. On the other hand, according to Mr. Sedgwick, when a change occurs in evolution in an animal which has no larval stage, in other words when a new adaptation is produced which is related to conditions existing throughout the independent life of the organism, then this variation or modification affects the whole constitution of the individual, has a retrospective influence on the embryonic development, and comes to be developed directly with no, or scarcely any, trace at any embryonic stage of the structural condition which must have preceded it in the line of descent. The two most marked instances of these contrasted modes of development cited by Mr. Sedgwick are (1) the existence of gill-clefts and gill-arches in the embryos of all air-breathing

vertebrates, and (2) the absence of any trace, in embryonic life, of the fore-limbs in snakes.

Embryologists will be aware that the theory so ably advocated by Mr. Sedgwick had already been suggested by Balfour. It is contained in the following paragraph (*Comp. Embryology*, vol. ii., p. 174):—

"Another point which deserves notice in the snake is the absence in the embryo of all external trace of limbs. It might have been anticipated on the analogy of the branchial arches, that rudiments of the limbs would be preserved in the embryo even when limbs were absent in the adult. Such however is not the case. It is however very possible that rudiments of the branchial arches and clefts have been preserved because these structures were functional in the larva (Amphibia) after they ceased to have any importance in the adult; and that the limbs have disappeared even in the embryo, because in the course of their gradual atrophy there was no advantage to the organism in their being specially preserved at any period of life."

Mr. Sedgwick has not extended his criticism to the question of recapitulation in larval stages themselves.

This however has been done by Mr. E. W. Macbride, who points out that according to the view we have been considering, however modified the record of ancestral history contained in the larval development may be, the embryonic record can never rise above it in value. This writer evidently, whether consciously or unconsciously, takes a Lamarckian view of evolution. He considers that so far as we can judge by comparative anatomy the stimuli to evolution, in the sense of change of structure, have been two (1) change of environment or habits, (2) increased or decreased demands on the working of certain organs. Larval stages according to Macbride are due to new stimuli commencing to act at a late period of life; in the case of flat fishes if the young when they emerge from the egg were at once to adopt the adult mode of life then their symmetrical larval stage would be omitted from their ontogeny. He considers that secondary larvæ must be regarded as having arisen owing to the young adults having taken to a new mode of

life. He instances as the best examples of this the aquatic larvæ of May-flies and dragon-flies, which have gills consisting of thin laminæ abundantly supplied with tracheæ. He then proceeds to consider in some detail the numerous larval forms of Crustacea and Echinodermata, and to draw conclusions concerning their ancestral significance.

We have then to rely for our conclusions concerning the evolutionary history of a form, or the course of modification it has passed through in descent, on the evidence of comparative zoology and palæontology, and in tracing lines of evolution and comparing them with the changes exhibited in the development of the individual, we are necessarily led to inferences concerning the modes in which modifications are produced. Conditions and structures exhibited in the embryo which are absent in the fully developed organism are in some cases, as we have seen, repetitions of a larval or temporary condition of the immediate ancestor. Further we know that in numerous cases such a larval stage is secondary and not itself an ancestral condition. Therefore neither the embryonic transient stage nor the larval stage by any means necessarily exhibits a condition of any adult ancestor. The general truth which we do find to hold good is that well-marked larval stages are associated with conditions of life differing from those to which the adult is subjected. Metamorphosis in the structure of the organism is observed to correspond to a more or less sudden and considerable change in the conditions of life. An organism may be adapted to one set of conditions throughout its independent life, or successively to different sets.

The fact that all the terrestrial Vertebrata, the Sauropsida and Mammalia, exhibit gill slits in the embryo at a certain stage is explained by the fact that they are all descended from ancestors which passed through an aquatic larval stage. The Amphibia at the present day pass through such a stage. It does not follow that the Amniota are descended from ancestors which were aquatic and branchiate in their adult condition. The actual history of the Alpine Salamander (*Salamandra atra*), shows us how, as an adaptation to terrestrial conditions, the offspring may be

retained in the uterus during the branchiate condition, and not be born until the metamorphosis has been accomplished. We have good reason to believe, however, that the transition to the Amniota from Amphibian-like ancestors was not effected in this manner, since viviparity even in Mammals was evidently acquired at a later stage, and the change came about by means of the development of an egg-shell in which the larva was contained and protected during its development. None of the existing Amphibia, though they exhibit various different methods by which the eggs are kept out of water during development, show any tendency to form an egg-shell. But it may reasonably be suggested that the formation of this structure was originally due in some way to the stimulation of the epithelium of the oviduct by the retention in it of a large-yolked ovum. Mr. Macbride distinguishes two classes of stimuli to evolution, change of environment, and increase or decrease of function, but it appears to me that all modifications may be described as the effects of stimulation, of which the increased or decreased activities of organs are particular cases. To my mind it is not possible to conceive the origin of the shelled egg as due to the selection of individuals in which the shell appeared as a variation, unless we have some idea of the cause of its appearance.

Judging from the structure of the aquatic larvæ of existing Amphibia, and from the general requirements of aquatic life, we may suppose that in the actual ancestors of the Amniota the free aquatic larvæ possessed a median membranous fin-fold. We do not, however, find that this or any trace of it is preserved in the embryo of the Amniota. Lateral fin-folds do not exist in the tadpole of the Batrachia, and we need not expect, therefore, to find them in the embryos of Amniota. But the disappearance of the median fin-fold indicates that the ancestral larval condition may undergo considerable modification when it becomes embryonic. The mere fact that they were functional originally in a free larval condition is probably not the whole explanation of the temporary development of a complete system of gill-arches and gill-slits

in the amniote embryo. Supposing that no functional importance in embryonic life belongs to them, it is to be noted that the embryonic branchial blood-vessels are metamorphosed into the vascular system of the adult, as they are in the metamorphosis of Amphibia, and a very considerable and very important part of them persists in the adult structure. This does not account for the persistence in the embryo of open branchial clefts, but even these do not wholly disappear in development. The first remains as the Eustachian tube, and even the posterior are related to the development of the thymus gland. It seems to be a general fact that a structure which in metamorphosis disappears completely may easily be omitted altogether in embryonic development, while one which is modified into something else continues to pass more or less through its original larval condition.

If the aquatic larval condition then was ever an adult ancestral condition it must have been the ancestor of Amphibian forms, and only through these the ancestor of the Amniota. We have therefore to inquire how far the larvæ of the Amphibia resemble the adult ancestors of that group. The important resemblances of a tadpole to a fish, and the evidence that fishes are older palæontologically than Amphibia, are sufficient to show that the latter are descended from fishes, and that the aquatic larva is not entirely a kainogenetic adaptation. But when we come to compare in detail the Amphibian larvæ with all known fishes we are forced to the conclusion that the larva is far from repeating any possible adult condition very exactly. If we suppose that the tadpole of the frog represents the adult ancestor of that form, we imply that that ancestor was entirely destitute of fin-rays and of paired limbs, and that the fore-limbs were originally evolved as outgrowths within the branchial chamber beneath the operculam. We should also imply that the piscine adult ancestor had no scales. Now the recent Dipnoi present an obvious approximation to the Amphibia, and we know that forms belonging, according to the structures capable of preservation in the fossil state, to the Dipnoi existed as early as the Devonian period. We do

not know how the paired limbs were transformed from the radiate to the pentadactyle form. But we consider it most probable that the Amphibia diverged at an early period from the Dipnoan stem, and therefore arose from ancestors which had fin rays in a continuous median fin, which possessed paired limbs like those of the Dipnoans, and scales or dermal ossifications. It is more probable that the Amphibian larva has lost its paired limbs and fin rays since the adult form was evolved, than that the adult ancestor never possessed paired limbs and that the pentadactyle limbs were evolved independently of the paired fins of the Dipnoi. The Amphibian larva has also lost all trace of scales or other dermal ossifications. The extinct Amphibia called Labyrinthodonts possessed dermal osseous plates, and the existing Cœciliidæ possess scales. The larva of the frog therefore, instead of recapitulating the ancestral condition has lost nearly everything characteristic of a fish except the pharyngeal branchiæ, which it could not lose without ceasing altogether to be an aquatic larva. The larva therefore is much more of an adaptation than a recapitulation.

At a time when the doctrine of recapitulation had more influence on phylogenetic inquiries than it has now, W. K. Parker observed characters in the tadpole of the Anuran *Xenopus* (*Dactylethra*) which he considered more obviously ancestral than those of the common frog. He regarded the skull and the tail as remarkably chimæroid. The tail he said terminated in a long pointed lash, the fin membrane ceasing at some distance from its end. Mr. Beddard found on examining specimens of this tadpole hatched in the Zoological Gardens, that the fin membrane really continued to the extremity of the tail, but was very narrow, and the description of Parker was a mistake due to the contraction of the membrane in spirit specimens. There are other peculiarities however in the *Xenopus* tadpole in which it differs from the larva of the frog. The mouth is terminal, there are no suckers on the chin, and the fore-limbs do not develop beneath the opercular fold. These differences show so many features in the frog larva which must be regarded as special modifications in that form.

We must infer from these facts that the Amphibian larva only resembles the ancestor so far as the conditions of its life resemble those of the ancestor, and differs so far as its conditions of life are different from those of the ancestor. Selectionists of course will see nothing in this inconsistent with their views of modification. They will say that the larva and the adult have varied independently and the fittest have survived in each case. But in this as in many other cases it is important to notice that we have no evidence that the required variations ever occurred except when the conditions of life changed. The mere statement that the modifications occurred and survived because they were advantageous is not sufficient. Supposing that the modifications occurred in certain individuals while all the rest died, then we ask how and why did they occur in those individuals. So long as we regard the individual as a single definite form like a house or a vase, it may appear conceivable that the modifications of individuals are due to changes arising in the germ cell, to blastogenic variations, and that the adaptation of individual to conditions of life is due to the selection among a host of slightly different individuals of those which most approach the suitable structure. But when, as in the case of the frog, we see the same individual always passing in development through two quite distinct stages of life, which are adapted to two incompatible conditions, aquatic and terrestrial, we find it much more difficult to form a conception of the mode in which such a metamorphosis could have been brought about by blastogenic variations. Supposing it to be possible by always breeding from the individuals with the smallest limbs to produce a race or species without limbs at all, it does not follow that it is possible to produce by selection a race in which there are no limbs during the first half of life, and well-developed limbs in the second half. But this is what we have in the frog. It may be said that the two stages are so marked and distinct as to vary independently as though they were separate races, and therefore a different standard of selection can be applied to each. But this simply means what the Lamarckian contends for, namely, that the modifications are

always associated with differences in the conditions of life. If the conditions of life have nothing to do with the origin of variations then the variations of the fins in the two stages of the Amphibian will be the same as in the Dipnoan which lives under nearly the same conditions all its life. Only the standard of selection will be different. But it is impossible to believe that the selection of individual variations such as occur in the Dipnoans could produce a form in which there were two stages of life, one without limbs and the other with well-developed pentadactyle limbs. There is no evidence that such a thing is possible.

On the other hand we have plenty of evidence that conditions of life acting temporarily during a particular period of life produce definite changes which disappear when different conditions act upon the same individual. Muscles and skeletal structures diminish when disused and increase when exercised. As far as the individual is concerned, apart from inheritance, we know that adaptation of structure to different conditions of life at different periods of life actually does take place. It cannot be denied that the process of evolution so far as we are able to elucidate it is such as would result if such changes as are produced by conditions in the individual were inherited, if successive states corresponding to successive modes of life tended to recur in every generation, so that the effects of conditions were cumulative. The Dipnoan ancestor of the Amphibian was able to respire air by means of its air-bladder. Reaching places where the air was moist, but water in any large bodies scarce in summer, it would be forced to depend more on air breathing, and less on its gills. The latter would be more or less dried and, therefore, undergo retrogressive changes. The air-breathing adult would deposit its eggs in small bodies of water where want of room, the persecution of enemies, and the scarcity of animal food would force the larva to live among water-weeds and live upon them. It would cease to use its paired fins, and cease to exercise the muscles and rays of the median fins. The larva would, therefore, on Lamarckian views, become degenerate. According to those views, development of organs depends

very largely on the stimulation applied to them in the struggle for existence in successive generations of individuals. In the larva of the frog the limbs and fin-rays ceased to be stimulated by exercise, and consequently developed less and less in this period of life. In adult terrestrial life, on the other hand, the paired limbs were constantly used, and the stimulation thus caused would produce its effect at the corresponding period of life in the development of the limbs in the adult form at the end of the larval period.

We may next consider recapitulation in the development of fishes. A classical instance of this is the development of the tail in certain Teleosteans. The primitive condition of the tail is the symmetrical condition, in which the fin membrane is continued round the end of the notochord, and supported internally by cartilaginous rays, outside which, beneath the epidermis, are very numerous thin horny fibrous rays uniformly close together. This condition existed in the earliest Elasmobranchs, for instance, in *Pleuracanthus*. In the majority of Selachians from the Carboniferous to the present day, without any fundamental modification of the character of the skeletal ray-supports, there is an alteration of the shape of the fin. The ventral portion is enlarged to a greater or less degree in comparison with the upper, and so forms a ventral lobe of the fin, the original terminal portion forming the dorsal lobe.

In the osseous fishes, which general term includes Ganoids, Teleosteans and Dipnoi, there is an important modification of the skeleton which extends to the skeleton of the tail. Dermal calcifications derived from the scattered tubercles of the Elasmobranchs unite to form bony fin-rays outside the horny fibres. These at the bases of the rays correspond in position to the cartilaginous median rays, while distally they branch and correspond more with the original horny fibres. With the appearance of this modification the tail may retain its original symmetrical or diphycercal condition as in several Devonian Ganoids, in the modern *Polypterus*, and in both ancient and modern

Dipnoi. In other cases as in the Sturgeon and many other Ganoids the hypertrophy of the ventral lobe produces the heterocercal condition. Finally, in Teleosteans, the upper lobe or original terminal portion of the tail is aborted altogether, and the vental lobe becomes terminal and acquires a secondary symmetry. It is unnecessary on the present occasion to trace the extent of recapitulation in all the various cases. It will be sufficient to refer to the homocercal Teleosteans, for example, the Pleuronectidæ, Clupeidæ, or Salmonidæ. In these the larva has at first a symmetrical membranous tail without fin-rays. In this minute radiate fibres appear, which clearly corerspond to the horny fibres of Elasmobranchs and Ganoids. The cartilaginous rays are but little developed in the fin itself, but the basal portions within the trunk, that is the epural and hypural cartilages are developed and soon replaced by bone. When the dermal fin-rays appear they are from the first developed on the ventral side behind the termination, and the terminal portion never develops them. This terminal portion is bent up by the hypertrophy of the ventral lobe and becomes rudimentary.

Thus in these fishes the tail is at first diphycercal, then in development passes through a heterocercal condition and afterwards acquires the secondary symmetry called the homocercal condition.

Two zoological thinkers have recently made endeavours to ascertain the advantages of the various forms of fishes' tails in adaptation to different circumstances. They do not refer to the origin of the different forms, but to their mechanical, or adaptational value. This in itself is of great importance and interest, and to the zoologist who thinks in the terms of selection the use or advantage of each form appears to be the explanation of its evolution. F. E. Schultze develops his views in connection with a consideration of the tails of the Ichthyosaurians which are heterocercal, but with an asymmetry which is the reverse of that seen in fishes. The terminal portion of the vertebral column in these reptiles was bent downwards, and on the upper side of it was a somewhat triangular cutaneous fin, in

addition to the dorsal fin in the middle of the back. It is surprising that the true structure of the tail in these animals, discovered by Fraas of Stuttgart in 1892, is not described in that generally excellent work the *Royal Natural History*, where the obsolete view that the tail was horizontal like that of Cetacea is repeated.

Schultze points out that in the heterocercal tail the more expanded lobe is the more flexible, while the continuation of the vertebral column is much more rigid. Consequently when the tail is moved horizontally the flexible lobe will yield to the resistance of the water, and the surface of the whole tail will be inclined to the horizontal plane, and will move not horizontally but towards the more rigid edge, that is in the case of sharks or sturgeon, upwards. Everyone knows that an oar inclined under water and moved horizontally will rise to the surface or go deeper into the water according to the direction of the inclination, and the same thing happens when a feather in which the vane is broader on one side of the axis than the other is moved under water. The greater flexibility of one sides causes the feather or heterocercal tail to take an inclined position and therefore always to move away from the horizontal plane towards the more rigid edge. Consequently the tail of the fish in which the upper lobe is more rigid rises when it moves. As the fish is at the same time propelled forwards, the effect of this would be to ram its snout into the ground, and to counteract this it only needs to raise the edge of its pectoral fins, the resistance of the water will then raise the fore part of the body and the whole fish rises from the bottom. According to Schultze this is the object of the arrangement; the fish being heavier than the water requires a mechanism to enable it to swim easily from the ground. The Ichthyosaur on the other hand was specifically lighter than the water on account of its lungs and blubber, and therefore needed a motor mechanism to counteract its tendency to rise. Its tail when in motion sinks, and it only needed to lower the front edge of its pectorals, to descend to greater depths when it pleased.

The relations of the fins in the flying fishes (Exocœti),

and certain other Scombresocidæ are analogous. The tail is homocercal, but the ventral lobe is distinctly larger and stiffer than the dorsal. Physiologically therefore the tail acts like that of Ichthyosaurus. Here however the counter-action cannot be produced by the pectorals, because they are too long and too weak, and moreover are observed to be folded against the sides of the body in rapid swimming. The necessary effect is produced by the pelvic fins, the specific gravity of the flying fish being less than that of the water.

Ahlborn takes a somewhat different view. He considers that there are important advantages in the action of heterocercal tails which Schultze has not perceived. In his opinion the bottom fish requires to have a tail which will rise in order to prevent it rubbing against the ground in its stroke and therefore failing to propel the fish when the latter desires to put itself in motion. In the case of the surface animal, Ichthyosaur or flying-fish, a symmetrical tail might when put into motion at the surface pass into the air, and so the creature would become for the moment helpless; it therefore requires a tail which will tend to pass more deeply into the water. He calls the ordinary heterocercal tail epibatic, the symmetrical tail isobatic, and the tail with reversed heterocercy hypobatic.

It is clear that none of these considerations help us to understand how on Lamarckian principles the various forms of tail arose, and even with regard to function it seems to me that the two authors mentioned have overlooked some of the most important points. It seems to me that the chief use of a heterocercal tail to a fish that lives near the bottom is the very fact that such a tail throws the hinder end of the body up and keeps its nose on the ground, for it is on the ground that it finds it food. It is a remarkable fact that the heterocercal tail is usually associated with a snout projecting beyond the mouth, and such a snout is in a large number of cases, if not in all, used for routing in the ground in the search for food. Such is certainly the case in the sturgeon, and it is true of some at least of the Selachians; *Scyllium canicula* and *catulus* feed on lower

animals which conceal themselves in the ground at the sea-bottom, and probably use their snouts in hunting for prey, although I am not acquainted with any particular observations on the performance of such actions by them. On the the other hand it may be objected that a large number of Selachians are as pelagic and active in their habits as any fishes, never use their snout for probing the ground, but pursue other active fishes in mid-water. This is true of the common spiny dog-fish, *Acanthias vulgaris*, and of the large species of Carcharias living in tropical seas. I cannot pretend to be able to explain all the difficulties presented by such species, but it is certainly a fact that there are among them differences in the degree of prolongation of the snout, and that when the mouth is nearer to the end of the head, the tail is more bent up so as to approach the homocercal condition. This correlation is evident enough in *Læmargus borealis*, the Greenland shark, and in *Selache maxima*, the basking shark. Concerning the aperticolous habits of the latter there can be no doubt, since it lives on plankton, while the Greenland shark has a great avidity for whale's flesh, and also devours fishes.

It is a remarkable fact that the most ancient Selachian forms of which anything like complete remains have been preserved do not resemble the recent forms in the characters of snout and tail. The mouth in them is terminal, and the tail either diphycercal or nearly homocercal. In *Pleuracanthus* we find the former condition; in *Acanthodes*, the ventral lobe of the caudal fin is well developed while the upturned caudal extremity of the body is short, so that we have an approach to a secondary symmetry which in *Cladoselache* of the Lower Carboniferous becomes remarkably perfect, the dorsal and ventral lobes being equal, although the dorsal is still formed not by fin-rays but by the upturned extremity of the trunk.

Such facts as these strongly suggest that it is possible to over-estimate the importance of chronological position in interpreting the evolution of animal forms. Certain adaptations are found in unexpected perfection in geological periods which have been supposed to be characterised

by generalised forms corresponding to the diagrams of primitive ancestors invented by the ingenious morphologist. As we are forced to modify our earlier views by additional evidence we become more and more convinced that it is not length of time which is so important in organic evolution, *i.e.*, in the modification of structure, but change of the conditions of life. There can be no doubt that the heterocercal condition of the tail in fishes has been derived from the diphycercal, but the latter is scarcely less common at the present day than it was among the fishes of the Palæozoic age. In both cases it appears to exist in connection with certain habits, certain modes of swimming, which are not confined to one kind of habitat. Thus we find it in more or less perfect development in *Chlamydoselache*, which is a deep-water shark, in *Protopterus* which is a Dipnoan living in rivers, and the Ganoid *Polypterus*, likewise a fluviatile fish. In all these cases the movement of the fish seems to be rather slow, and horizontal in direction.

To return to the heterocercal tail. It exists both at the present day and in former periods, back to the Palæozoic, among the fishes now united under the name Teleostomes, formerly separated into the two divisions Ganoids and Teleosteans. Instead of these two divisions we have now the two sub-divisions Crossopterygians and Actinopterygians, distinguished by the structure of the paired fins, the former having fringed fins, the latter fan-shaped fins. The heterocercal tail is quite as exclusively characteristic of the Actinopterygians as the structure of their paired fins. Both types have persisted from the Palæozoic period to the present day, but the Teleosteans with homocercal tails are undoubtedly connected by a series of intermediate forms with the heterocercal Actinopterygians. The question then which we have to consider is whether there is evidence that the earlier heterocercal Actinopterygians sought their food upon the bottom.

In answer to this question we can say that fossil forms similar to the sturgeon are very ancient. In *Palæoniscus* the snout is slightly produced beyond the jaws but not so much as in the sturgeon. It is found in the Permian. But

in the majority of the Palæoniscidæ and Platysomidæ the mouth is terminal, and although the tail is heterocercal it approximates in most cases towards the homocercal condition in the fact that the ventral lobe is so large as to be equal or nearly equal to the dorsal lobe which contains the upturned extremity of the vertebral column.

In the Dapediidæ, Pycnodontidæ, Caturidæ and Leptolepididæ, which are represented principally in Mesozoic strata, we have obviously the forerunners of the homocercal Teleosteans, and in them the homocercal condition of the tail practically complete.

If as I have suggested the benefit of the heterocercal tail lies in the effect it has of throwing the hinder end of the body upwards when it is moved, still the lateral motion of the tail could not give a stimulus to the hypertrophy of the ventral fin-rays. The origin of the modification must be sought in some particular stimulation of these rays. Such a stimulation might well be produced by the direct movement of the rays themselves. There is in fishes a movement of the rays by the muscles attached to them, in addition to the movement of the caudal region by the lateral trunk muscles. My theory therefore is that the development of the heterocercal tail from the diphycercal was due to the concentration of active exertion in the ventral fin-rays, so that in course of generations these were hypertrophied and the others atrophied. The object of this exertion is assumed to be the raising of the tail and the depression of the head in fishes which fed upon the bottom. The lobe having once been hypertrophied the further modification in fishes which moved actively, even when they ceased to feed on the bottom, and swam chiefly in a horizontal direction, would take the form of a further modification in the shape and position of the ventral lobe until the homocercal condition was attained.

It is a remarkable fact that although the Pleuronectidæ and Gadidæ have generally been considered to be so similar that they have been placed in the same order Anacanthini, the structure and development of the tail described above occur in the flat fishes but are entirely

wanting in the Gadidæ. In the latter the tail is permanently diphyceral, it is composed of dorsal and ventral rays which are equal in number and size, and in fact closely resembles the tail of the extinct Cœlacanthidæ. There can be little doubt that even if the Gadidæ cannot be directly derived from the latter family they are descended from Crossopterygian Ganoids with diphycercal tails, and have never passed through a heterocercal condition. Although the structure of the tail in the Gadidæ was briefly and correctly described by Alexander Agassiez in his paper on the "Development of the Tail," he did not attach sufficient importance to it, believing that a very slight apparent upbending of the termination of the notochord showed the essential similarity in the development of this type of tail with that seen in other Teleosteans. The proper classification of the Anacanthini is yet to be worked out, but there can be no doubt that the Gadidæ and Pleuronectidæ, instead of being closely allied, are very remote from each other in structure and descent.

The recapitulative development of the tail in many Teleosteans by no means proves that the larval condition as a whole in those forms represents the condition of an adult ancestor. We do not find that the scales in development pass through an Elasmobranch and then a Ganoid stage. On the contrary, they are developed directly. There can be little doubt that the larvæ hatched from pelagic eggs, as well as the eggs themselves, are a direct adaptation to the conditions of life of marine fishes. It is not possible at present to say what are the conditions which tend to increase the number and diminish the size of eggs, but pelagic eggs are smaller and more numerous than those which are attached to solid objects in fresh water or in the littoral region. The pelagic larva presents many peculiarities which are obviously not ancestral, among them the fusion of the veins of the yolk-sac into one continuous chamber surrounding the yolk and communicating with a wide opening at the hinder end of the heart. This may be explained without difficulty on Lamarckian principles as the result of the small quantity of mesoblast available at the

very early stage in which the larva has to begin to obtain its food. The early use of the jaws, muscles, and sense-organs would cause their precocious development, so that the quantity of mesoblast surrounding the yolk-sac would be reduced, and thus the veins could no longer at this stage be divided from each other.

No Ichthyologist doubts that the fishes with closed air-bladders have been derived from forms in which the bladder opened from the gullet or other part of the intestines. The Physostomi retain other primitive characters besides the opening of the air-bladder, for example, the posterior position of the anus and of the pelvic fins. In the Anacanthini and Acanthopterygii the position of the anus is more anterior, and the pelvic fins instead of being placed in the hinder region of the body are, in most cases, either below or actually in front of the pectoral fins. According to the law of recapitulation we should expect to find that the larvæ of the two groups were similar in the position of the anus and the origin of the pelvic fins. But this is not the case. In the physostomous larva the anus is near the end of the tail, and separated by a considerable interval from the yolk-sac, while in the physoclist larva the rectum and anus are immediately behind the yolk-sac, and far in front of the end of the tail. The explanation here appears to be that in the adult the anus has been pushed forward by the increased use and consequent increased development of the ventral fin (so-called anal fin), and that the new condition is developed directly because there is no influence in larval life tending to retain the ancestral condition. The ontogeny of the pelvic fins in the Physoclisti is more recapitulative, but not completely so. The fins when they first appear are small dermal folds behind the pectoral fins, but they very soon pass to the position which they occupy in the adult. It is not very easy to discern the probable causes of the alteration in the position of the pelvic fins either on Darwinian or Lamarckian principles, but we may reasonably suppose that the particular position of these fins in the adult has been determined by certain requirements of attitude and movement in the fish. The mechanical conditions

of the movement of a fish in the water are not very definitely known. But the selectionist must assume that the position of the pelvic fins is a mechanical advantage, and if that is the case the change of position would necessarily be produced on Lamarckian principles by the directions in which the muscles were exerted.

Among particular cases of metamorphosis in fishes none is more remarkable or has attracted more attention than that of the flat-fishes. This has always been cited as a conspicuous case of recapitulation, as it certainly is. But it also illustrates very forcibly the principle here maintained, that recapitulation of modifications of structure depends not merely on heredity, but to a very important extent on recapitulation of changes of condition. The pelagic larva of *Pleuronectes*, *Solea* or *Rhombus* is very closely similar to that of the Gadidæ or of many Acanthopterygians. We may well believe that this pelagic larval condition had been acquired before the peculiar condition of the flat fishes had been evolved. The larval symmetrical condition represents therefore not the adult condition but the larval condition of the ancestor. New conditions of life and consequent modifications of structure have been introduced into the adult stage of life, while the conditions and the structure of the larva have remained unchanged. Whether the habit of lying on the bottom on one side was originally acquired at an early or a late age, it is certain that it has come to be assumed at a very early age, and consequently the structural changes which we know to be associated with it are now in great part simultaneous with the ordinary development of the adult structures of the fish. For this reason it is by no means easy to ascertain from the ontogeny of the flat fish, much as the process has been studied, the characters of the adult ancestors. The assumption of the special Pleuronectoid characters is most retarded in species of Rhombus and their allies, such as the turbot and brill. In these cases we find stages in which the eyes are still symmetrical when the fin-rays are well developed, and we see a symmetrical fish with a morphologically heterocercal tail, a single dorsal and a single ventral fin, neither extending so far forward as

in the adult flat fish, and dermal spines somewhere on the head. These dermal spines are additional evidence of the want of affinity between the Pleuronectidæ and Gadidæ. In searching for the possible ancestors of the flat fishes among extinct forms, we find the required characters most clearly represented in the Pycnodonts, a compact group which ranged from the Lias to the Eocene, in which latter formation fossil flat-fishes first appear. The Pycnodonts have a single dorsal and single anal fin, and each of these in some genera is much extended antero-posteriorly. The body also is compressed laterally and rhomboidal in shape. But it is doubtful whether the specialised dentition of the Pycnodonts could have given rise to the dentition of the Pleuronectidæ.

The precise nature of the changes which have taken place in the flat-fish in its modification from a symmetrical fish is as follows. The orbital region has been twisted so that the interorbital septum is brought round to the upper side, and the eye of the lower side to the upper. It cannot be said that we can point out with certainty the muscular efforts or mechanical strains which would produce changes in this direction in the individual as an acquired character. The action of the eye-muscles would probably have some effect, and the weight of the fish resting on the ground would force the lower eye-ball towards the upper side and so distort the face. In all probability both these influences have contributed to the result. If acquired characters are not inherited, at least evidence and logic force us, whether we will or not, to the conclusion that the modifications which have led to the condition of the eyes in flat fishes were determined by the mode of life which these fishes adopted. There is no evidence known to me which supports the view that such modifications, or variations which could lead by accumulation to such modifications, could possibly arise independently of the influence of external conditions.

Another modification which has occurred is the extension of both the dorsal and ventral fins in an anterior direction. The ventral fin is extended towards the head, pushing the anus before it, and passing ventral to the

viscera and abdominal cavity. The dorsal fin extends on to the head, its base being attached, not to the median line of the head, which is bent by the distortion of the eyes, but along the outer edge of the orbit belonging to the lower side, this edge being now in line with the dorsal edge of the body. This extension of the dorsal fin separates both eyes and orbits entirely from the lower side of the head, and adds greatly to the disguise beneath which the original symmetry of the fish is concealed. The increase in the extent of the median fins corresponds to the increased use which is made of them in the peculiar habits of the flat-fish. The lateral muscles of the body and tail are no longer constantly employed in locomotion, but the fish glides over the bottom by means of an undulating motion of its marginal fins. This motion involves the constant action of the numerous small muscles attached to the fin-rays. Such an action commencing in the individual at a period when the differentiation of the fin-rays from the embryonic tissue belonging to the fins was not completed, would tend it is believed to increase the development of such embryonic tissue and differentiate an increasing number of rays from it, while the direction of the musular strains, the constant endeavour by muscular contraction to draw forward the anterior ends of the fins, would determine the direction of their extension. Thus the mode in which the fins were used would produce in the course of generations the structure and relations which they now possess.

The third chief general peculiarity of the flat-fishes is the absence of pigment from the skin of the lower side, an absence which has been shown by experiment to depend on the absence of light. It is a fact that pigment is developed on the lower side of these fishes when that side is exposed to light, and it is also a fact that when such exposure is maintained the lower side does not develop pigment so quickly or so abundantly as the upper side. It is maintained that the former fact proves that the character was originally acquired by the individual, the latter that it is now strongly inherited.

There are certain conditions of life which have produced

a similar effect on animals most remote from one another in structure and systematic position. Complete or nearly complete, and constant darkness is one of these conditions. Two modifications which are generally observed in animals living in darkness are diminution in the pigmentation of the skin and deterioration of the eyes. In most cases there is abundant evidence that the animals passing their lives in darkness have but recently diverged from forms which live in daylight. We may inquire then to what extent the ancestral condition is recapitulated in the ontogeny of these forms, with regard to the two adaptations mentioned. Not long ago this question was raised in a controversy concerning the possibility of explaining the loss of the eyes in cave-inhabiting animals by the selection of individual variations. Professor Lankester had suggested that the individuals which had the best eyes were better able to find their way out of the dark recesses into which they were accidentally carried, because they would detect a glimmer of light which those whose eyes were less perfect would not notice, and the former moving towards the source of the light would emerge into the open air again. It seemed to me that this hypothesis was contradicted by the fact of the recapitulation of the eyes, because when very young all the individuals are able to see, and would therefore all be able to escape in the manner suggested.

But we must turn to the results of direct observation in order to ascertain to what extent this is correct, whether the eyes are fully developed in the immature stages of cave animals which are blind when adult. Unfortunately observations on the ontogeny of such animals are by no means complete or detailed, but still enough has been ascertained to show that recapitulation is neither perfect nor altogether wanting.

Troglocaris Schmidtii is a crustacean of the caves of Europe, which is quite blind in the adult condition; it was found by Dr. Joseph that the embryo while still within the egg was provided with eyes.

In the adult Proteus of the caves of Adelsberg in Dalmatia, the eyes are very small and entirely covered by the

skin. But in the young when it is first hatched the eyes are well developed.

Typhlogobius californiensis is a species of Goby living on the shore near San Diego in California. It lives usually in the holes of a burrowing carideoid crustacean, and has aborted eyes and a pink colour. The whole frontal region of the skull of this fish is much modified, the scales have entirely disappeared, and the spinous dorsal fin has been much diminished in size. In a small specimen ·9 in. long the eyes were visible and apparently functional, but in larger and adult specimens there is a thick layer of skin over the eyes so that the latter can scarcely be perceived, and certainly cannot enable the fish to see. The size of the eye was not however found to be obviously different in the smallest and largest specimens.

A detailed description of the minute structure of the eyes of this blind fish in the adult condition has been published by W. E. Ritter in America, but unfortunately he had no embryos or larval stages and therefore was unable to compare the condition of the eyes in the earlier and later stages of life or of the ontogeny. The smallest specimens examined were 19 mm. long or nearly $\frac{4}{5}$ in. and the largest 63 mm. or nearly $2\frac{3}{5}$ in. Comparison of the various specimens did not prove either a constant advance or a constant retrogression in the development of the eye between these sizes, but it is noteworthy that the only specimen in which the lens was entirely absent was one of the maximum size, 63 mm. in length. The usual condition of the eyes was the following. The epidermis over the eye is similar to the ordinary epidermis. Beneath this is dermal fibrous tissue also of the ordinary kind. Around the eye is a thin layer of denser tissue representing the sclerotic and cornea. The choroid is thin and rudimentary, in front of it is the pigment layer of the retina which is proportionally very thick and contains no cellular elements. In front of the pigmented layer is the cellular part of the retina which is but little differentiated; it contains however a layer of rods but no cones. The lens is present with the exception mentioned above, but the argentea is entirely absent, and

likewise the vitreous humour. Optic nerve and eye muscle are present but very slender and long.

In 1891 the eggs of this Goby were found attached to the lower side of the rocks beneath which the fish lives, and in the embryo before hatching the development of the eyes was found to be perfectly normal, and similar to that which takes place in other fish embryos.

In the eye of Proteus a progressive development of the lens in the embryo and its subsequent degeneration and total disappearance in the adult have been definitely observed by Schlampp (1892). It develops normally from the epiblast and sinks into the opening of the secondary optic vesicle where it is still to be found in the hatched larva. It does not advance however beyond the embryonic cellular structure, and in quite young animals is already much reduced in size; in the adult not a trace of it remains. The vitreous body is also absent in Proteus, the retina and optic nerve are present. The retina in consequence of the absence of the vitreous body does not spread out flat but forms a solid spherical mass whose histological structure is not markedly different from that of other Amphibia, but the terminal elements (rods and cones) do not reach their perfect form. In the Mole (Talpa) the lens is present though it retains its embryonic cellular structure throughout life, and in this respect is more rudimentary than the lens of Typhlogobius. The choroid is but slightly developed, and has little pigment, while the pigment layer of the retina is highly developed. The cellular layer of the retina is present but not fully differentiated; rods and cones according to Kohl are both present. The vitreous body is also present, and likewise the optic nerve, which Semper stated to degenerate in adult life.

Three species of blind crayfishes are known which inhabit subterranean waters in North America, in Missouri, Kentucky, and Tennessee. They are *Cambarus pellucidus*, Tellkampf; *C. hamulatus*, Cope and Packard; and *C. setosus*, Faxon. The eyes in these, to superficial observation, appear to be absent. The eye-stalks are present but they terminate in a blunt cone instead of a bulbous enlargement,

and no black pigment is visible at their extremities. Tellkampf as quoted by A. S. Packard in the *American Naturalist*, 1871, stated that the eyes were larger in the young of *C. pellucidus* than in the adult. Garman (1889) says that the eyes are more prominent in young specimens of *C. setosus*, and appear to lack but the pigment.

The minute structure of the eyes in the adult of *C. setosus* and *pellucidus* has been described in detail by G. H. Parker (1890), but I have not been able to discover that any investigation of the development or of the structure of the eyes in the embryos or young has yet been made. The optic stalks are not only pointed, but smaller than in eyed crayfishes. In *C. setosus* the end of the optic stalk is covered with an undifferentiated cuticle of uniform thickness, and similar to that of the rest of the body. No indication of the facets characteristic of functional eyes is present. The so-called hypodermis, the cellular layer beneath the cuticle, is also undifferentiated : the only feature in which the hypodermis of the retinal region differs from that of other regions is that it contains two or three irregular rows of nuclei instead of a single one. There is, however, below the hypodermis within the eye-stalk an optic ganglion of considerable size, and from this ganglion there passes a short narrow optic nerve which extends to the hypodermis. The complicated structure of the retina which exists in functional crustacean eyes has therefore completely degenerated, so that it has reverted to the condition of undifferentiated hypodermis. Pigment is entirely absent. The condition was observed in three specimens, two of which were 6 cm. long, the third 4·2 cm.

In *Cambarus pellucidus* the condition of the cuticle was the same, and the optic ganglion and nerve were present as in *setosus*, but the structure of the retinal region was different. Degeneration had not proceeded so far. The rudimentary retina connected with the optic nerve is thickened, forming a lens-shaped mass, which contains, besides nucleated cells like the ordinary hypodermis cells, large multinucleated granular bodies. Parker gives his reasons for considering these granular bodies as the de-

generate representatives of the groups of four cone cells each, which are present in normal retinulæ.

We have then in the case of the blind dwellers in darkness a physical condition which is uniform and constant throughout life, and a structural condition obviously related to it which is not direct but recapitulative in its development. The development of the eyes in these forms offers a marked contrast therefore to the entire absence of the forelimbs of snakes at all ages, and resembles the development of teeth in the gums of the fœtal whale. The following conclusions follow necessarily from the facts.

(1) The blindness of cave animals has certainly not been produced by the selection or survival of individuals in which the eyes were defective from their first development. If it is due to selection at all, it is the selection of individuals in which the eyes underwent progressive deterioration after the commencement of independent life.

(2) The eyes even in the stage in which they are most developed are far from being as well developed as in the ancestors which lived in daylight, but are only somewhat more developed than in the adult animal. Recapitulation does not therefore occur except when the external condition to which the ancestral structure was adapted continues to act at an early period of life.

In this case, therefore, as in many others, if we persist in applying the selection theory of evolution we must be content to infer that the variations occurred in particular ways without any particular reason. If hereditary variations are independent of the external conditions of life there is no reason why the eyes of blind animals should be better developed in the young than in the adult. It cannot be maintained that this is due to a general law of inferior variations, that the absence of selection allowed individuals with inferior eyes to survive and breed, and that congenital inferiority of an organ always manifests itself by its degeneration at a late period of life. On the contrary we know plenty of cases in which an organ is absent in the young and fully developed in the adult. The facts compel us to conclude that the ontogeny of the individual has been

modified in correspondence with the uniformity or the periodicity of the external conditions to which it is exposed, and we can only infer that the influence of the external conditions is the cause of the modifications. We have reason to believe that in the individual the total absence of light leads to a progressive deterioration of eyes, and if this progressive change, repeated in every generation, ultimately becomes hereditary, then it would begin earlier and proceed farther in successive generations. On this view the very imperfect and incomplete recapitulation which we actually observe is the necessary consequence of the fact that the animals are exposed throughout their ontogeny to complete darkness.

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